



Early Terrestrial Plant Environments: An Example from the Emsian of Gaspé, Canada

C. L. Hotton, F. M. Hueber, D. H. Griffing, and J. S. Bridge

The origin of embryophytes in the Ordovician and their subsequent radiation in the Silurian and Devonian were profoundly important events in the history of life. Land plants ameliorated an initially hostile terrestrial environment, paving the way for colonization by other organisms. Rhizoid and root activity reduced substrate instability, promoted chemical weathering, and increased nutrient availability; the establishment of a plant canopy dampened fluctuations in humidity and temperature, greatly augmented primary productivity, and opened up niches for exploitation by other organisms (Beerbower 1985). Increased incorporation of CO₂ into organic carbon by land plants over the course of the Siluro-Devonian was apparently a primary factor in precipitating a sharp drop in atmospheric CO₂ (Berner 1993, 1994; Mora et al. 1996; see chapter 10), which in turn was likely responsible at least in part for the Permo-Carboniferous glaciations. Even the Frasnian—Famennian marine mass extinctions have been attributed to coastal marine eutrophication fueled by tracheophyte radiation and evolution of deeply penetrating root systems over the course of the Devonian (Algeo et al. 1995; Algeo and Scheckler 1998).

Despite the significance of early land plant paleoecology, detailed studies of pre-Carboniferous plant assemblages are rare. A

few paleoenvironmental studies of specific plant assemblages have been conducted (Andrews et al. 1977; Gensel and Andrews 1984; Edwards and Fanning 1985; Scheckler 1986b; Kasper et al. 1988), of which the most detailed is that by Schweitzer (1983). However, these studies are limited by absence of sedimentological detail. Because the degree to which a fossil assemblage resembles the parent plant communities depends in large part on sedimentological and taphonomic processes, understanding the sedimentological context of fossil assemblages and associated facies is crucial to the reconstruction of their living environment. Hence, we have undertaken a detailed study of the sedimentology of fossil land plant assemblages in the Emsian age Cap-aux-Os Member of the Battery Point Formation, exposed along Gaspé Bay, Quebec, Canada. The diverse Gaspé flora has been studied for over a century, beginning with the pioneering work of J. W. Dawson (1859, 1871). Many subsequent studies have established it as one of the best-described floras of Early Devonian age (Hopping 1956; Daber 1960; Kräusel and Weyland 1961; Banks and Davis 1969; Banks et al. 1975; Hueber 1967, 1971, 1983b, 1992; Gensel 1976, 1979, 1984; Granoff et al. 1976; Remy et al. 1993; Stein et al. 1993). However, no paleoecological study of this flora has been attempted.

Although the fossil record suggests that by

the Emsian, embryophytes had occupied the land for roughly 70 million years (Gray 1993; Strother et al. 1996), terrestrial ecosystems at that time are still considered primitive. Absence of tetrapods and the plesiomorphic nature of arthropod faunas at this time suggest that plant-animal interactions would have been limited (Selden and Edwards 1990; DiMichele et al. 1992). Plants are believed to have occupied sites in rare sexual reproductive events and then formed monospecific stands through extensive vegetative growth (the "turfing-in" model of Knoll et al. 1979; Niklas et al. 1980). Interspecific plant interactions consequently would have been limited as well, and early land plants are considered to have exhibited relatively little niche specialization (DiMichele et al. 1992). They are further believed to have been restricted by their free-sporing life cycle and relatively inefficient water conducting systems to moist, mesic sites, unable to occupy high-stress (e.g., hydric or xeric) habitats (Scheckler 1986b; Bateman 1991; Algeo and Scheckler 1998). Some authors, nevertheless, place them in salt marshes, a physiologically stressful habitat (Schweitzer 1983; Retallack 1990; Edwards and Selden 1993). In our opinion, these propositions are best treated as null hypotheses about early land plant ecology, to be tested by independent data. It should be kept in mind that this generalized model is more applicable to early stages of land plant evolution. By Emsian time, land plants had diversified into at least three major tracheophyte clades (lycophytes, trimerophytes, and rhyniopsids *sensu* Kenrick and Crane 1997a) as well as, most likely, one or more bryophyte clades, suggesting concurrent ecological differentiation.

Our goal here is to test hypotheses about early land plant ecology against data derived from detailed biostratigraphic analysis of the Cap-aux-Os sediments. We first present data on floristics and taphonomy, then a summary of sedimentological evidence for overall depositional environment, as well as more detailed description and interpretation of depositional environments of plant megafossil assemblages. We have chosen to address the following issues in this

paper: (1) to characterize types of environments occupied by plants; (2) to search for consistent associations between plant taxa and environments; (3) to characterize the degree to which plant assemblages were in fact monodominant; (4) to investigate the extent to which early land plants were capable of occupying high-stress environments, focusing specifically on brackish water habitats. Finally, we document the taxonomic and diversity disjunction between megafloral and palynofloral records within the Cap-aux-Os Member, and we discuss its implication for estimating actual plant diversity and ecosystem complexity.

MATERIAL AND METHODS

More than 186 meters of stratigraphic section were logged in centimeter-scale detail along sea cliffs exposed near d'Aiguillon, Québec (figure 11.1). The strike and dip of the strata are such that lateral exposure of most stratigraphic units is limited to a few hundred meters. However, erosional irregularities in the coastline provide three adjacent exposures of one plant-rich mudstone interval near the base of the measured section. Three sections of this interval were measured (our Seal Rock Landing, Seal Rock West, and First Cove West localities) to construct a more accurate three-dimensional depiction of the strata (figure 11.1). Each rock unit was examined for grain size and color variation, primary sedimentary structures, pedogenic features, paleocurrent indicators, vertebrate and invertebrate faunal assemblages, and ichnofabrics. Samples of critical rock types and plant-bearing strata were prepared for petrographic examination and taphonomic and ichnologic analysis at Binghamton University. Photomosaics of key stratigraphic intervals were constructed to facilitate description of lateral variation in the strata. Polaroid images annotated in the field were later combined with the photomosaics to generate lateral bedding diagrams and facies distribution information. Paleocurrent orientations were corrected for tectonic tilt of strata using the stereonet method outlined in

Lindholm (1987). The sedimentary facies recognized were compared with those in modern sedimentary environments and comparable ancient deposits, to interpret depositional environmental conditions directly associated with plant habitats and burial settings. Only a brief synopsis of this work will be provided here. Full description and interpretation of the Cap-aux-Os Member facies will be published separately (Griffing et al. 2000).

Plant megafossils were collected from every productive horizon within the measured section. A total of 58 megafossil sites were collected. Where possible, large blocks were quarried, but in some cases only relatively small hand samples could be collected. Identification of plant taxa from each site was made first on whole-rock specimens in the laboratory, after degasing if necessary. A representative subsample from each horizon was selected and bulk macerated in hydrofluoric acid for spore samples and to identify additional small, fragmentary, and minor components of the horizon. Some identifiable material from bulk macerations was subjected to additional oxidative treatment, either with Schulze's solution (saturated potassium chlorate in concentrated nitric acid) or warm dilute potassium hydroxide. In many cases, naturally retted material was sufficient for observing cellular details. Selected specimens were dried from 100 percent ethanol and mounted on stubs for observation and photography on Hitachi S-570 and Leica Stereoscan 440 scanning electron microscopes (SEM).

The digested material from every bulk maceration was prepared for dispersed spores (heavy liquid separation, residues bleached for 6 to 8 minutes, and mounted in glycerine jelly). In addition, every unoxidized horizon within the measured section was collected and prepared for dispersed spores. Approximately 200 to 600 grains were counted and identified per sample. Information on dispersed spore assemblages in this paper is based on 60 samples from the lower half of the measured section. A paleoecological analysis of the dispersed spore assemblage of the Cap-aux-Os Member will be presented elsewhere. For comparison of *in situ*

spores with dispersed spores, sporangia were mounted with no additional treatment on stubs for SEM. For light microscopy (LM), some sporangia were subjected to Schulze's solution followed by ammonium hydroxide, washed, and mounted in glycerine jelly. Other sporangia were mechanically crushed, bleached for about 7 minutes, and mounted, to standardize comparison with dispersed spores.

Additional information on the sedimentology and paleontology is drawn from observation of laterally equivalent sediments exposed along the beach west of Gros Cap-aux-Os in Forillon National Park and in correlative units exposed on the south shore of Gaspé Bay (figure 11.2). Of particular interest is an extensive sandstone unit on the south shore with abundant plant remains permineralized by CaCO_3 . This unit correlates with the Cap-aux-Os Member on the north shore (McGregor 1973, 1977), and in this chapter it will be referred to as the permineralized sandstone plant assemblage.

REGIONAL GEOLOGICAL SETTING

The Battery Point Formation is part of the Gaspé Sandstone Group, a coarsening-up clastic wedge developed on the southern edge of Laurussia, 10° to 20° S latitude in Emsian times (Scotese and McKerrow 1990). As a consequence, climate was presumably tropical (Witzke 1990). In the absence of reliable biological climate markers, sedimentology alone can contribute little to understanding of climatic conditions during the deposition of the Battery Point Formation, except that rainfall was moderate, judging from the absence of calcretes and sedimentological evidence for perennial rivers. The Battery Point Formation is exposed on both north and south shores of Gaspé Bay (figure 11.2); however, detailed correlation between strata on the two shores is currently not possible because of facies differences. On the north shore, three members have been recognized (Brisebois 1981). Our measured section is from the middle, mudstone-dominated Cap-aux-Os Member, as it is richest in plant fossils (figure 11.2). The age of the

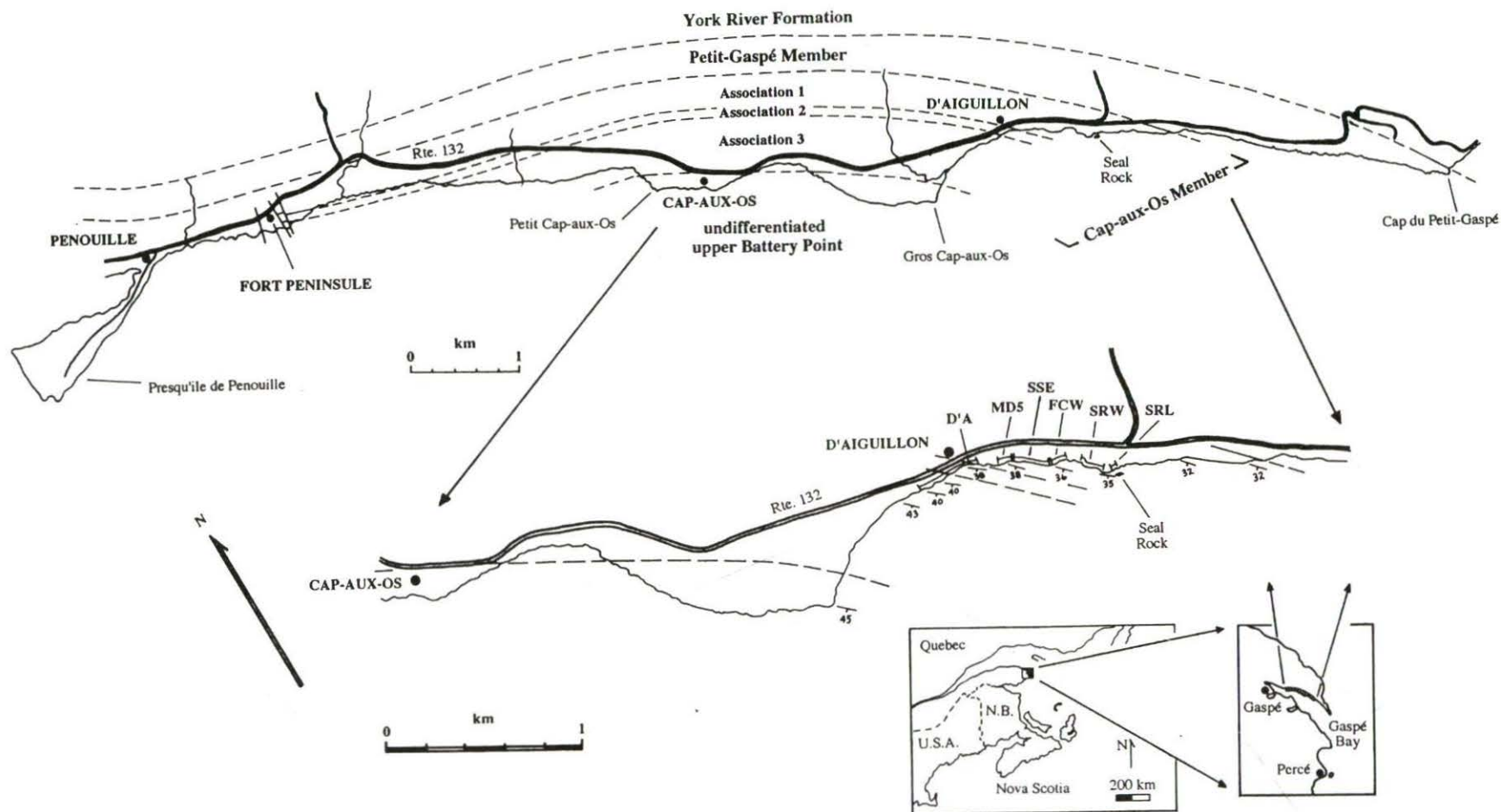


Figure 11.1.

Map of study area, depicting distribution of members of Battery Point Formation, and measured sections on the north side of Gaspé Bay (after Lawrence 1986). Sections referred to in text: D'A, d'Aiguillon; MD5, Mudstone 5; SSE, Sandstone E; FCW, First Cove West; SRW, Seal Rock; SRL, Seal Rock Landing.

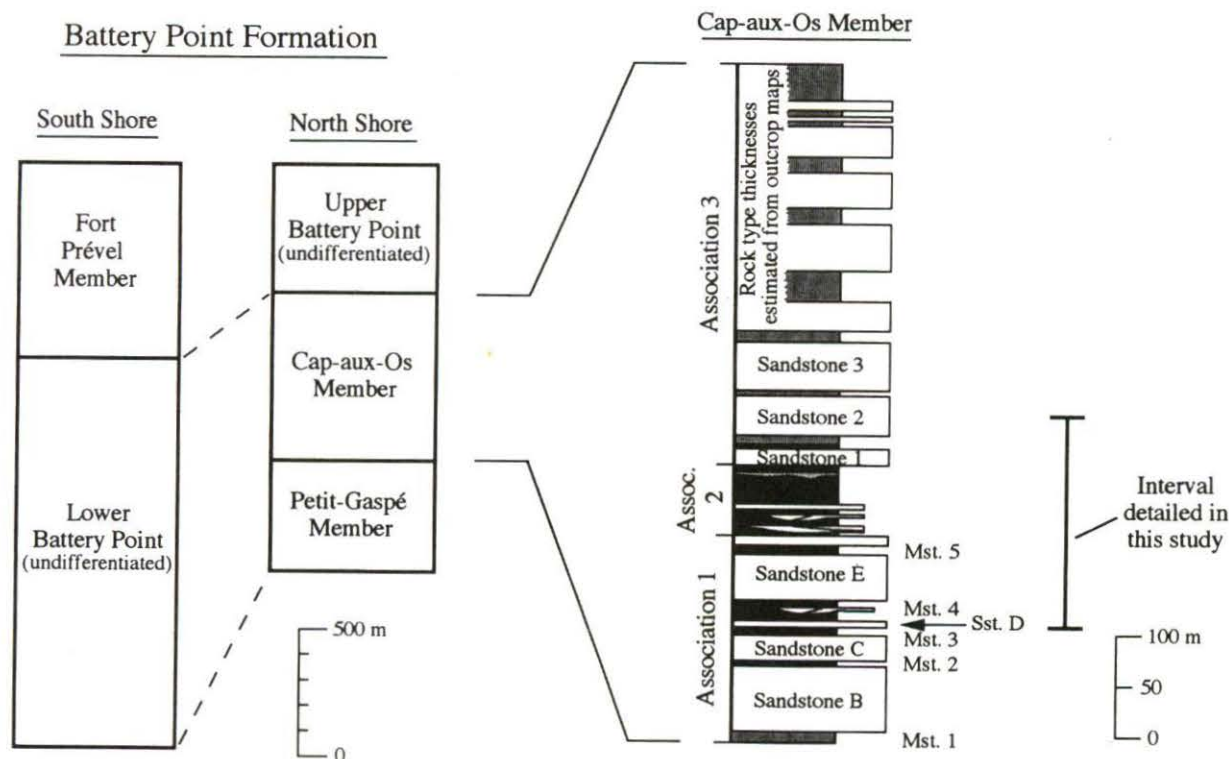


Figure 11.2.

Inferred correlation between exposures of Battery Point Formation on the north and south shore of Gaspé Bay, and generalized measured section on north shore of Gaspé Bay, based on the internal stratigraphy of Lawrence (1986) and the study described in this chapter. *Stipple*, red mudstone intervals; *black*, gray mudstone intervals.

Battery Point Formation is early Emsian to early Eifelian, based on data from brachiopods (Boucot et al. 1967) and spores (McGregor 1973, 1977; Richardson and McGregor 1986). The measured section falls within the early to late Emsian *annulatus*–*sextantii* spore assemblage zone of Richardson and McGregor (1986).

FLORISTICS AND TAPHONOMY

Approximately 18 species of embryophyte megafossils have been recognized within the Cap-aux-Os Member, including two possible bryophytes, two probable gametophytes, six zosterophyll species, one lycopsid, two species of rhyniopsid, and at least five species of trimerophytes (table 11.1). Details of the taxa may be found in the appendix to this chapter and the associated figures. Common taxa include *Psilophyton*, *Pertica*/*Trimerophyton*, *Huvenia*, *Crenati-*

caulis, *Sawdonia*, and *Sciadophyton*. Zosterophylls, even as fragments, can be identified to species level on the basis of their distinctive cuticle. Trimerophytes are readily recognized as a group from fragmentary vegetative material, although identification to species level requires relatively complete specimens. Two other organisms, *Prototaxites* and *Spongiophyton*, are also important constituents of the flora. We interpret both as eumycetous fungi. *Prototaxites* has recently been reinterpreted as a gigantic perennial fungal body analogous to a modern bracket fungus (Hueber 1996). Anatomically preserved specimens of *Spongiophyton* from the south shore permineralized sandstone assemblage, consisting of septate hyphal tubes surrounded by a thick resinous “cuticle” of apparently agglutinated hyphae, have been interpreted as lichens (Stein et al. 1993).

Consideration of taphonomy of fossil assemblages is essential to any reconstruction of their growth environment. Assemblages reflecting

**Table 11.1. Megaflora of Cap-aux-Os Member
and associated dispersed spore taxon (where known)**

<i>Plant megafossil</i>	<i>Dispersed spore taxon</i>
Embryophyta <i>incertae sedis</i>	
New genus A (?hepatic)	?
<i>Sciadophyton</i> spp.	N/A
New genus B	N/A
New genus C	?
Rhyniopsida	
<i>Huvenia</i> sp. nov.	<i>Retusotriletes</i> or <i>Calamospora</i>
" <i>Taeniocrada dubia</i> " (new genus D)	?
Lycophytina	
<i>Drepanophycus spinaeformis</i> Goeppert	<i>Retusotriletes</i> or <i>Calamospora</i> ^a
<i>Crenaticaulis verruculosus</i> Banks et Davis	<i>Retusotriletes</i> spp.
<i>Renalia hueberi</i> Gensel	<i>Retusotriletes</i> spp.
<i>Sawdonia ornata</i> (Dawson) Hueber	<i>Retusotriletes</i> spp.
<i>Zosterophyllum</i> sp.	<i>Retusotriletes</i> spp.
New genus E	? <i>Retusotriletes</i> ^b
" <i>Bathurstia</i> " sp. (new genus F)	?
Trimerophytes	
<i>Psilophyton dawsonii</i> Banks, Leclercq et Hueber	<i>Apiculiretusispora arenorugosa</i> morphon
<i>P. forbesii</i> Andrews, Kasper et Mencher	<i>A. arenorugosa</i> morphon
<i>P. princeps</i> (Dawson) Hueber ^c	<i>A. arenorugosa</i> morphon
<i>Pertica varia</i> Granoff, Gensel et Andrews	<i>A. arenorugosa</i> morphon
<i>Pertica</i> sp.	<i>A. arenorugosa</i> morphon
<i>Trimerophyton robustius</i> (Dawson) Hopping	<i>A. arenorugosa</i> morphon

?, unknown, or questionable; N/A, not applicable.

^a Spores have been extracted from fertile specimens of *Drepanophycus spinaeformis* from New Brunswick (Li et al. 2000).

^b Based on spore masses from a monodominant assemblage of new genus E.

^c Reported by other authors but not found in this study.

minimal transport [autochthonous or parautochthonous—i.e., transported but still within life environment (Bateman 1991)] are essential to interpret growth habitat, habit, and associations. We judge that roughly 35 of the 58 megafossil assemblages in the Cap-aux-Os Member are either autochthonous or parautochthonous. Evidence of minimal transport includes evidence of anchorage, axes oblique or perpendicular to bedding plane, and preservation of complete axes with fine detail. Other authors have noted that early land plant assemblages are often preserved in parallel alignment along the bedding plane, as though plants were rooted at one end in the process of burial by the enclosing sediment (Andrews et al. 1977; Edwards 1979a). Observation of axes undulating in parallel suggests that they were anchored (presumably rooted) at one end, leaving the other ends

free to become aligned to water currents. Regular spacing of aerial axes, especially characteristic of large trimerophytes, again suggests attachment to a horizontal stem or rhizome that is no longer preserved. That axes branch through the bedding plane is another strong indicator of *in situ* burial, since this position is not energetically stable under most conditions of transport. Examples of this include aerial axes of *Sawdonia ornata* at the type locality, and stalked gametophores of *Sciadophyton* and new genus B that extend through the bedding plane into superjacent sediments. The preservation of delicate structures such as distal branch tips, buds, and attached sporangia suggests limited transport, although the degree of resistance to fragmentation and degradation that these plants may have displayed is unknown because of the lack of taphonomic analyses of appropriate analogues.

Most important, among the major classes of tracheophytes identified from the measured section (lycophytes, trimerophytes, rhyniopsids), none appear to have exhibited significant differences in preservation potential.

SEDIMENTOLOGY

Facies Associations

Lawrence (1986) recognized three facies associations within the Cap-aux-Os Member (figure 11.2). The lowermost of these associations (Association 1) contains 4- to 60-m-thick, multistory sandstone bodies separated by thinner, red- and gray-mudstone-dominant intervals. Association 2 is dominated by gray mudstones at d'Aiguillon but also contains decimeter- to meter-thick sandstone sheets, and lenses and meters-thick, single-story sandstone bodies. Relatively coarser-grained, multistory sandstone bodies with uncommon, thinner red mudstone intervals characterize the uppermost association (Association 3) of the Cap-aux-Os Member. Paleocurrent indicators within the sandstones in the measured section at d'Aiguillon suggest unidirectional flow to the north and west, but a few strata indicate opposing paleoflow directions (Lawrence 1986; see following paragraph and figure 11.3). Most of the *in situ* and *in loco* plant megafossil horizons lie within the mudstone-rich portions of upper Association 1 and throughout Association 2 (figure 11.3), whereas highly fragmented assemblages occur in the multistory sandstone bodies.

Mudstone-dominant intervals contain a variety of distinctive features, including (1) meters-thick sandstone sheets and lenses that fine or coarsen upward, and that indicate paleoflow directions to the northeast to southeast, as well as to the north and west; (2) centimeter-scale, lenticular, wavy, and flaser bedding with wave-ripple and current-ripple marks (figure 11.4A); (3) centimeter- to decimeter-thick sandstone sheets containing wave-ripple marks, *Diplocraterion*, *Skolithos*, and *Phycodes*-like traces, and disarticulated cephalaspid fish skeletons (figure 11.4B,C); (4) desiccation-cracked mudstones with articu-

lated lingulid brachiopods (figure 11.4D); and (5) dark gray shales and siltstones bearing acritarchs, small bivalves, or small, thin-shelled lingulid, orthid, and rhynchonellid brachiopods.

Overall Environmental Interpretation

The Cap-aux-Os Member is interpreted as fluvial and delta-plain deposits (Lawrence 1986; Lawrence and Williams 1987; Bridge et al. 1998; Griffing et al. 2000). Paleocurrents suggest that the rivers transported sediment seaward to the northwest. Whereas Lawrence (1986) interpreted most of the multistory sandstone bodies in Association 1 as deposits of high-sinuosity river channels, marine or marginal-marine trace fossils (i.e., *Diplocraterion*) in the upper portions of Lawrence's Sandstones B, C, and D (Association 1, figure 11.2) suggest close proximity to the sea. Furthermore, the single-story sandstone bodies in Association 2 strongly suggest deposition in the form of channel bars and fills very close to the tidal limit of tidally influenced channels (Bridge et al. 1998; Griffing et al. 2000). Features of the mudstone-dominant intervals of Associations 1 and 2 just listed also suggest a coastal plain setting, with levees and crevasse splays, freshwater marshes and lakes, lacustrine deltas, brackish marshes and interdistributary bays, and sandy and muddy tidal flats (Griffing et al. 2000). The easterly directed paleocurrents are interpreted as flood tidal currents. These types of marginal marine deposits have also been described from the Catskill clastic wedge in New York and Pennsylvania (Bridge and Droser 1985; Halperin and Bridge 1988; Bridge and Willis 1994).

Plant-Bearing Facies

Most *in situ* and *in loco* plants in the Cap-aux-Os Member lie within two types of facies sequence: (1) at or near the base of 1- to 2-meter-thick, coarsening-upward sandstone sheets or lenses (Facies A), and (2) within the uppermost portion of 4- to 5-meter-thick, fining-upward single-story channel sandstone bodies (Facies B). Examples of both types of sequence occur

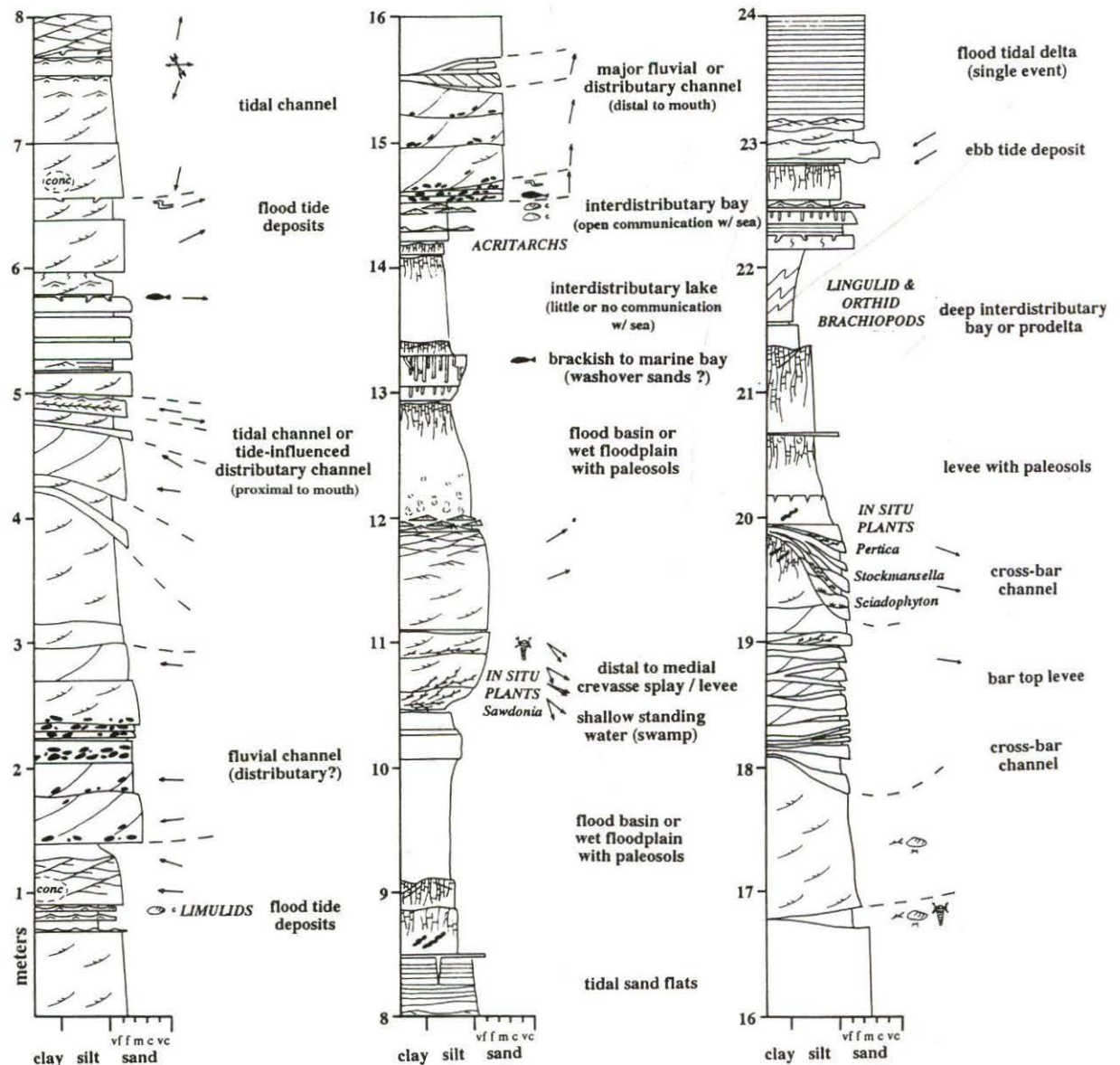


Figure 11.3.

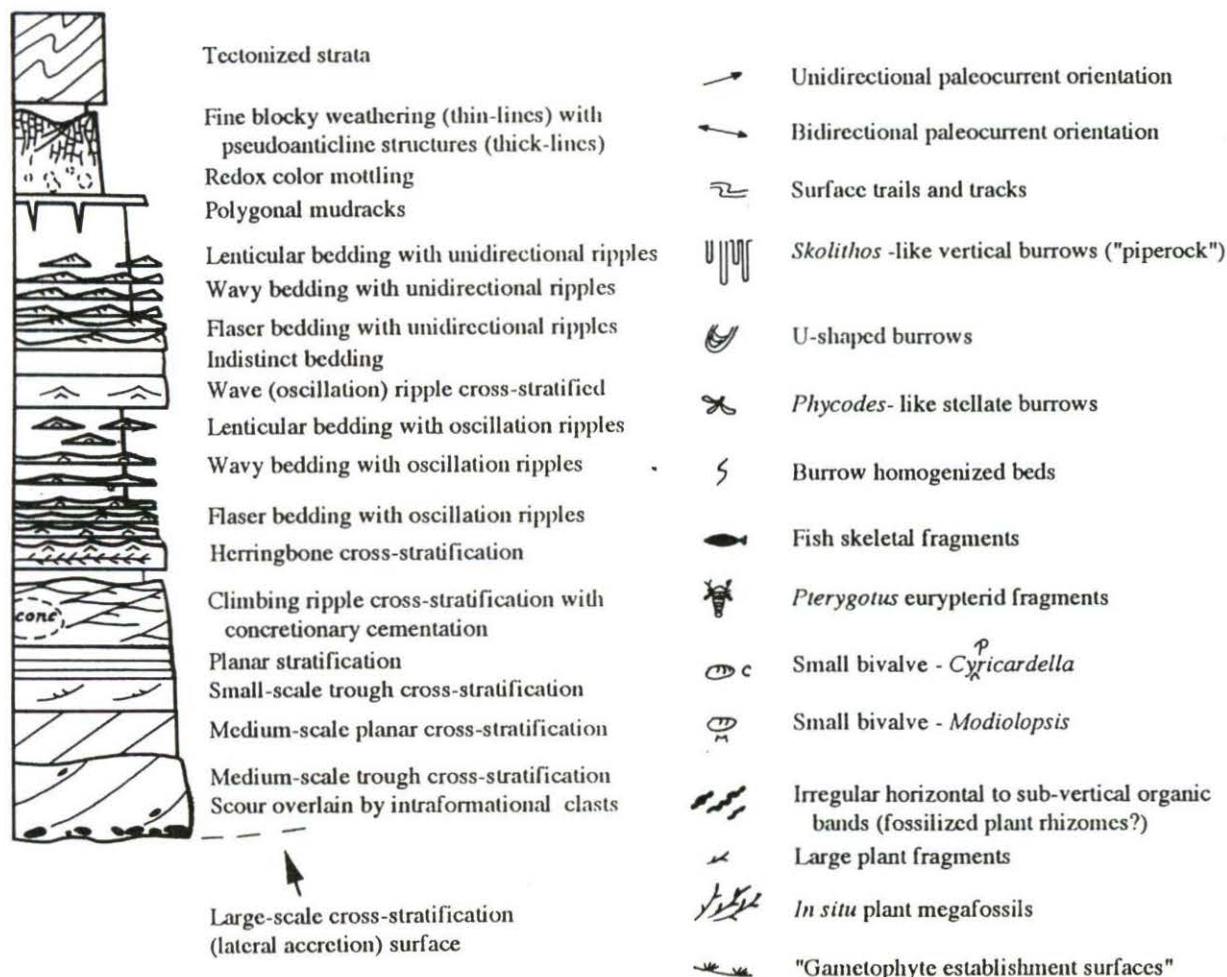
Detailed log of base of Association 2 (top of Association 1 is at 3 m mark). See text for further details. See p. 187 for key to symbols used.

within the lowermost 19 meters of Lawrence's Association 2 section at d'Aiguillon: the *Sawdonia ornata* type (Hueber 1971) and the *Pertica varia* type localities (Granoff et al. 1976), respectively (figure 11.5). In addition, a distinctive transported assemblage of *Spongiophyton* and *Prototaxites* occurs within the fine-grained portions of the multistory channel sandstone bodies in Associations 1 and 3 (Facies C).

Description of Facies A

The type *Sawdonia ornata* horizon is situated at the base of a coarsening-upward sequence of dark green-gray, silty claystones, to light green-gray, fine-grained sandstones (figure 11.3A, meters 10 to 12), like several other *in situ* zosterophyll occurrences in Association 1 and 2. This sequence is 1.7 m thick at the base of the exposure and tapers laterally upslope to about 0.5

KEY



m thick (figure 11.5). Dusky red-gray siltstones and dark green-gray mudstones underlie the *Sawdonia* horizon. The dusky red-gray siltstones have blocky fabric with slickensides and weakly developed pseudoanticline structures (i.e., vertic paleosol features). These siltstones contain carbonized, boudin-like structures that lie parallel to one another on the bedding plane but produce short lateral branches that plunge several millimeters into the bedding plane (figure 11.6A). We tentatively interpret these as plant rhizomes. Overlying the rhizome-bearing beds are dark green-gray mudstones that contain weakly developed blocky fabric (also interpreted as paleosol features; see also Elick et al. 1998b). A discontinuous, extensively weathered claystone interval

occurs at the base of the plant accumulation; it resembles the underclays of Carboniferous cyclothems in North America and Europe (Dulong and Cecil 1989). Waxy, dark green-gray mudstones above the underclay contain dense accumulations of toppled *Sawdonia* axes. These mat-like accumulations of horizontal axes extend along the entire outcrop and create localized paper coals (figure 11.6B).

A sheet-like to lenticular, coarsening-upward sandstone body directly overlies the *Sawdonia* mat. The lowermost 30 cm of this body grade upward from mudstone to small-scale cross-stratified, fine-grained sandstone. Numerous anchored plant axes that protrude upward through the siltstones and sandstones indicate unidirectional flow to

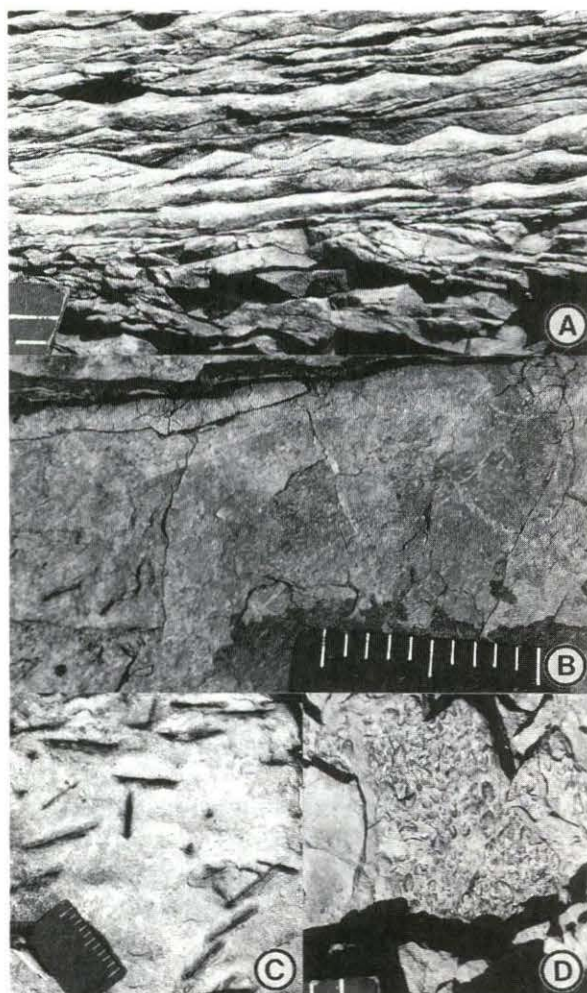


Figure 11.4.

A: Wave-rippled flaser-bedded sandstones, showing net migration direction (leftward) opposite to that of underlying medium-scale tabular cross-strata, Association 2 at d'Aiguillon. (1 cm scale, *lower left*.) **B:** Bedding-plane view of a muddy siltstone containing *Skolithos*-like vertical tube traces (white spots) and desiccation-crack polygons, Lawrence's Mudstone 4, Association 1 at exposures on the west side of Seal Rock Point (SRW) (1 dm scale). **C:** Upper surface of a white to buff medium sandstone bed displaying protrusive U-shaped burrow identified as *Diplocraterion*, Lawrence's Mudstone 4, Association 1 at First Cove West (FCW) west of Seal Rock Point (1 dm scale, *lower left*). **D:** Articulated but transported lingulid brachiopods forming one of several thin concentrations within gray mudstones with large polygonal mudcracks, lower portion of Lawrence's Mudstone 5 interval, Association 1 east of d'Aiguillon. (1 cm scale, *lower left*.)

the east and southeast (figure 11.6C). Some of the longer axes display several abrupt bends to a shallower angle at the base of sandstone beds,

before curving upward again. *In situ* *Sawdonia* axes terminate approximately 35 cm above the clay seam at the base. This coincides with the coarsest sandstone within the unit. Axes of a large trimerophyte with laterals stripped, and fragments of *Sawdonia*, *Crenaticaulis*, *Zosterophyllum* sp., *Drepanophycus*, and other taxa are common within the upper portion of the coarsening-upward sequence. These very fine to fine-grained sandstones are dominated by climbing-ripple cross strata (angle of climb up to 13°).

The coarsening-upward sandstone body is directly overlain by (1) fining-up, dusky red-gray siltstones with light green redox mottling and blocky fabric; (2) dark green-gray mudstones with weakly developed blocky fabric; (3) decimeter-thick beds of dusky red and green-gray siltstone featuring *Skolithos* and U-shaped traces, and disarticulated fish bone; and (4) a 32-cm-thick bed of dark gray shale with wave-rippled lenses of siltstone, containing numerous acritarchs at the base and millimeter- to centimeter-sized bivalves (? *Cypricardella*) throughout (figure 11.3).

We have identified at least 10 additional *in situ* plant horizons associated with this type of coarsening-upward sequence. Like the type *Sawdonia* sequences, most of these coarsening-upward sheets and lenses vary from decimeters to meters in thickness. One such sequence in Mudstone 4, Association 1 (see figure 11.2) has a triangular cross section. The upper portions of some of these sequences also include features not displayed in the *Sawdonia* example, such as meter-scale channel forms, wave ripple cross-stratification, and extensive disruption by burrows.

Interpretation of Facies A

Environmental interpretations of the lower d'Aiguillon section are provided with the stratigraphic log (figure 11.3). Basal mudstones display features typical of floodbasin muds with weakly developed paleosol horizons (e.g., vertisols, inceptisols, and entisols: see also Elick et al. 1998b). The underclay and waxy claystone underneath the *Sawdonia* mat and other plant assemblages most likely represent swampy gley



Figure 11.5.

Facies A and B at d'Aiguillon. Outcrop of Facies A siltstone/sandstone beds associated with *Sawdonia ornata* type locality (center), overlain by Facies B sandstones associated with the *Pertica varia* type locality (upper left). [2 m ranging pole (far left) for scale.] This and other photographs of outcrops are rotated so that beds appear to lie horizontal; actual dip about 30°.

soils with the O horizon preserved (Burrman 1975; Retallack 1990). The overlying wedge-shaped to lenticular, coarsening-upward sequence possibly represents the episodic progradation of a crevasse splay/levee into an adjacent floodbasin, which would have buried plants in place. An alternative origin, in view of the easterly directed paleocurrents, may be progradation of a coastal washover. At the *Sawdonia* site, the bends and successive upward curvature of axes through the strata point to persistent growth through several episodes of burial. Wave-rippled and/or burrow-modified beds in other coarsening-upward sequences of Facies A imply standing water for longer periods of time after a flood event. The overlying mudstones represent deposition of floodbasin muds punctuated by brief incursions of brackish or marine standing water. The dark gray shales at the top of the mudstones overlying the *Sawdonia* assemblage (figure 11.3, 11 to 14 m) are interpreted as interdistributary bay deposits with limited transport of coarser sediments during storms or river floods. The brief appearance of acritarchs in these dark gray shales indicates a short-lived marine incursion into the muddy bay.

Facies B: Type *Pertica varia* Site

In situ accumulations of *Sciadophyton*, *Huvenia*, and the type occurrence of *Pertica varia* (Granoff et al. 1976) are found within the uppermost beds of the 5.5-meter-thick, fining-up channel sandstone body directly above the type *Sawdonia* sequence (figure 11.3, 14 to 20 m). The basal medium-grained sandstones contain abundant intraformational mudclasts and cephalaspid and acanthodian fish bone fragments. Most of the sandstone body comprises a single set of large-scale inclined strata (i.e., a single story), where each decimeter- to meter-thick, large-scale stratum fines upward and laterally as it climbs to higher levels in the sandstone body. Associated with these fining trends within the large-scale inclined strata, medium-scale trough and planar cross-stratifications grade into small-scale trough cross-stratified fine-grained sandstones (figure 11.5). Paleocurrents are directed to the north in the lower half of the sandstone body.

The upper portion of the sandstone body consists of lenticular beds of small-scale trough cross-stratified, fine to very fine grained sandstones with a dominant paleocurrent orientation to the

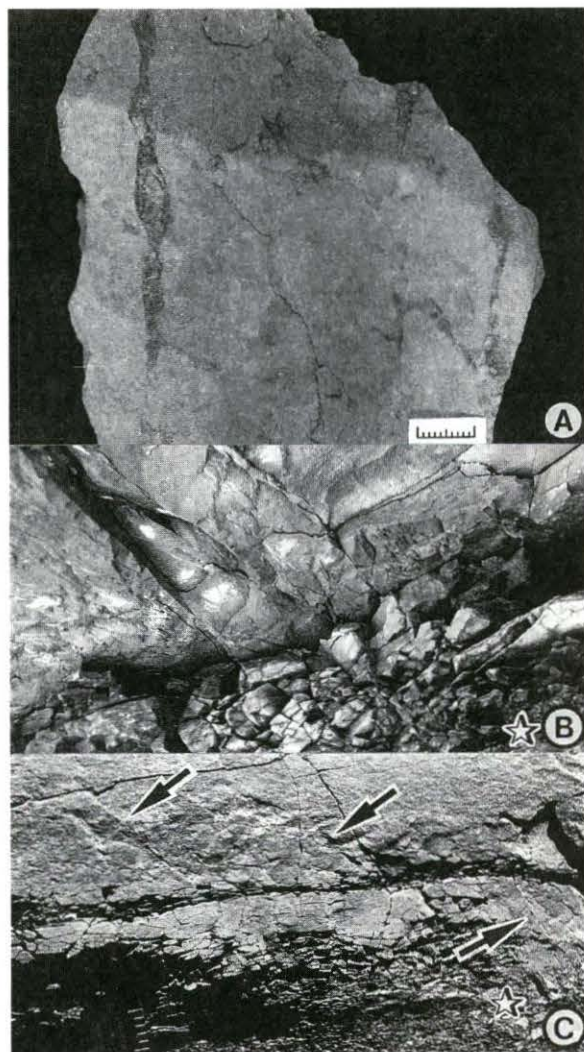


Figure 11.6.

A: Subparallel boudin structures covered with a thin carbonaceous film, preserved parallel to the bedding plane and bearing short lateral branches that plunge through the bedding plane, interpreted as rhizomes. Stratigraphic location of specimen is noted in figure 11.5 ("rhizome" bed). (1 cm scale, lower right.) **B:** Oblique underside view of basal sandstone bearing *Sawdonia ornata* at type locality. Note the subparallel axes of *Sawdonia* protruding upward through sandstone (toward SE, upper left). Base of plant occurrence highlighted by star. (Frame of photograph approximately 1 m across.) **C:** The same interval as shown in (B) from a cross-sectional view. Base of plant occurrence in claystone is highlighted by star. Notice traces of axes (arrows) bend to the left (SE) above a thin mud drape. (5 cm scale, lower left.)

east. These fine-grained sandstones also contain abundant fragmentary zosterophyll and trimerophyte axes, as well as disarticulated modiolosid and mytiloid bivalves and fragmented

eurypterid cuticle. Small channel forms (40 to 80 cm deep, 1 to 3 m wide) transect the small-scale cross-stratified sandstones in the uppermost part of the sandstone body. Channel fills typically contain very fine to fine-grained sandstone beds or dune-shaped lenses separated by medium green-gray shaly partings that are often occupied by *Sciadophyton*, and more rarely, by *Huvenia* (figure 11.7A). Plant axes bend in a preferred easterly direction. Large axes of *Pertica varia* also appear to be anchored in mudstone and are toppled in the same preferred easterly orientation.

The sandstone body is directly overlain by dusky red-gray siltstones containing redox mottling and desiccation cracks, and by dark gray to dusky red-gray mudstones with blocky fabric and pseudoanticlines. A strongly tectonized black to dark gray shale containing acritarchs, lingulids, and poorly preserved articulate brachiopods caps the sequence (figure 11.3, 21 to 22 m).

Facies B: Pyritic Sandstone at Seal Rock

A similar fining-upward sandstone sequence crops out on the east (SRL) and west (SRW) sides of Seal Rock Point and along the west side of the first cove to the west (FCW) (see figure 11.1). Like the type *Pertica varia* occurrence, *in situ* and *in loco* plant occurrences in the pyritic sandstone are located in the upper fine to very fine grained sandstone beds capping a channel-form sandstone body. *Drepanophycus*, *Pertica* and *Trimerophyton*, *Huvenia*, *Crenaticaulis*, and *Sciadophyton* occur on shaly drapes separating small-scale cross-stratified sandstone beds within small channels. *Sciadophyton* is undoubtedly *in situ*; its radially directed axes often display evidence of current reorientation in a preferred direction (figure 11.7B). Other plants within this sequence are most likely *in loco*; growing along channel margins, they were dissociated from the substrate and transported a short distance as attached clumps, often with axes displaying current reorientation (figure 11.7C).

The pyritic sandstone sequence is overlain by heterolithic mudstone and sandstone sheets that vary considerably in thickness among the

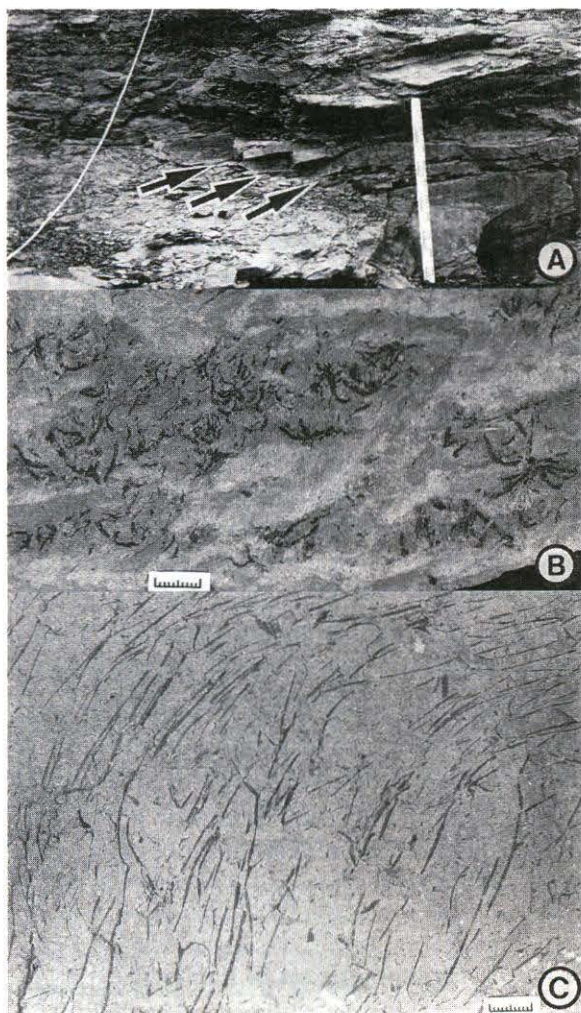


Figure 11.7.

A: Uppermost portion of single-story channel sandstone at the *Pertica varia* type locality. *Sciadophyton* occurs on clay drapes within shallow medium-scale cross-strata (arrows) (1 dm color bands on the ranging pole for scale). **B:** Plan view of *Sciadophyton* concentrated on lee face of small dune form, upper portion of pyritic sandstone, First Cove West. Note that axes, normally arranged in a radial pattern, show preferred orientation in the direction of the current activity that buried them (1 cm scale, lower left). **C:** Axes swirled in response to current action (?*Renalia* or ?*Eogaspesia*) from Facies B, upper pyrite sandstone, Lawrence's Mudstone 4, Association 1, Seal Rock Point (1 cm scale, lower right).

three sections. These strata display wave-rippled flaser to lenticular bedding and desiccation cracks (see figure 11.4B). Centimeter- to decimeter-thick sandstone sheets within this interval display small-scale cross-stratification with wave ripples and abundant U-shaped traces like *Diplocraterion* (figure 11.4C) and densely

packed *Skolithos* traces. Lingulid-rich siltstones are also common.

Facies B: Type *Renalia hueberi* Site (Fort Péninsule)

A variant of Facies B is exposed within a red mudstone interval of Association 3 near Fort Péninsule, west of d'Aiguillon (figure 11.1). *In situ* axes of *Renalia hueberi* (Gensel 1976) occur in a 3-m-thick channel fill in the uppermost portion of a 6-m-thick, fining-upward sandstone body. Unlike the *Pertica varia* and pyritic sandstone sequences, this fining-up sequence exhibits an abrupt change from medium- and fine-grained sandstone with medium-scale cross-stratification to 1- to 3-cm-thick alternations of purple-gray, small-scale cross-stratified coarse siltstone and mudstone in the channel fill.

Anchored *Sciadophyton* occurs on the top surface of almost every coarse siltstone bed in the channel fill. Elongate axes of *Renalia hueberi* protrude up through the intercalated mudstones, many displaying a weak preferred orientation to the north or northwest, but commonly reoriented to the east or northeast at the top of each mudstone interval, directly below the next siltstone bed. The brick red-brown mudstones above the sandstone body have extensive disruption and fine blocky weathering, as well as redox color mottling, slickensides, and pseudo-anticlines. No beds in this sequence contain invertebrate concentrations or traces commonly associated with marine environments.

Interpretation of Facies B

Facies B strata represent laterally migrating channel-bar and channel-fill deposits, and each set of large-scale inclined strata represents deposition from a discrete flood event (Griffing et al. 2000). At the *Pertica varia* type locality, the upper fine-grained sandstone strata and small channel fills containing *in situ* plants represent bar-top and cross-bar channel environments. Burial of plants by flood flow deposits was followed by establishment of plant communities in low, wet areas. Dune surfaces with mud drapes within

cross-bar channel fills display little evidence of long-term exposure (e.g., desiccation cracks or extensive burrowing), and in places, they display small wave ripples, indicating very shallow standing water. Paleocurrent and lithofacies variations within this type of sandstone body indicate the influence of tidal currents (see also Lawrence and Rust 1988). The lower parts of the channels were dominated by river currents and by ebb-tidal currents, whereas the upper parts were dominated by flood-tidal currents. This type of current segregation is typical of the strongly asymmetrical tidal currents expected in the channels near the tidal limit of estuaries and tidally influenced deltaic distributaries. The distribution of grain size and sedimentary structures is also typical of tidal channel bars near the fluvial–tidal transition: medium-scale cross strata limited to lower (subtidal) parts of bars; dominance of small-scale cross strata and relatively high proportions of mud in the upper, intertidal parts. The plant-bearing strata contain virtually no acritarchs or marine trace fossils, even though immediately adjacent strata do (see later discussions). Therefore, although the plants were probably buried *in situ* by deposits of tidal flood currents, there is no evidence of fully marine conditions in this facies.

In situ plant horizons in both the pyritic sandstone and *Pertica varia* type examples of Facies B are bounded by obvious tidal facies, which is once again suggestive of near-coastal, tidally influenced channels. The type *Renalia hueberi* site represents a muddy channel fill that formed after channel abandonment. The siltstone/ mudstone alternations probably represent periodic flood deposition, when relatively weak unidirectional flows carried a small amount of fine-grained bed-load through the abandoned channel. However, the *Renalia hueberi* channel fill is overlain by a paleosol, indicating a subsequent floodplain setting.

Description of Facies C:

Spongiophyton/Prototaxites Sandstones

Fragments of *Spongiophyton* and *Prototaxites*, along with fragmented plant “hash,” commonly

occur within the upper, finer-grained portions of 10- to 50-m-thick, very coarse to fine-grained sandstone bodies in Lawrence’s Associations 1 and 3. These bodies are multistoried and the stories are bounded by relatively major erosional surfaces with extraformational conglomerates and intraformational breccias. The *Spongiophyton* assemblage occurs in two stratigraphic settings: (1) as paper-thin drapes along medium-scale cross strata, and (2) in centimeter-thick intervals of planar stratified and small-scale cross-stratified, very fine to fine sandstone capping some sandstone stories. Plant fragment concentrations commonly develop a limonitic stain with weathering and were presumably partially pyritized. This assemblage is notably absent from bar-top facies in mudstone-dominant intervals (such as Association 2), yet it is common in upper Battery Point strata exposed on the south shore of Gaspé Bay (e.g., the permineralized sandstone assemblage). Its frequency of occurrence increases upsection in the Cap-aux-Os Member, along with an increase in average grain size and abundance of extraformational pebbles above basal erosion surfaces.

Interpretation of Facies C

The multistory sandstone bodies of Associations 1 and 3 represent channel-bar and channel-fill deposits of the main river channels that migrated across the coastal plain. The fragmentary *Spongiophyton* assemblage was transported from fully terrestrial settings inland and was deposited in the channels from decelerating floodwaters.

PALEOBOTANY AND PALYNOLOGY: RESULTS

Facies–Plant Associations

Facies A, B, and C are each characterized by a distinctive plant association (table 11.2; note that not all plant occurrences could be categorized within one of these facies). Zosterophylls and lycopsids are especially characteristic autochthonous components of Facies A. Of 11

Table 11.2. Facies/plant associations

	Taxon			Facies
	A	B	C	unclassified
<i>Sawdonia ornata</i>	4	1	—	—
New genus E (zosterophyll)	3	—	—	—
New genus B (gametophyte)	3	—	—	1
<i>Drepanophycus spinaeformis</i>	2	2	—	—
<i>Renalia hueberi</i>	—	3	—	—
<i>Crenatacaulis verruculosus</i>	—	4	—	—
Trimerophytes	—	7	—	1
<i>Huvenia</i> sp. nov.	—	4	—	—
<i>Sciadophyton</i> spp.	2	5	—	—
New genus A (?hepatic)	—	—	—	1
<i>Spongiophyton</i> sp.	—	—	15	—
<i>Prototaxites</i> sp.	—	—	5	—

examples of Facies A, eight are occupied by *Sawdonia*, new zosterophyll genus E (see appendix, figure 11.16C,D), *Drepanophycus*, or *Renalia*, and three others are occupied by new genus B, a putative gametophyte (see appendix, figure 11.12A, C–E). Trimerophytes occur in the coarser, transported fraction of Facies A, in the crevasse-splay and levee sandstones that bury autochthonous zosterophylls. We have noted four examples of this kind of occurrence, including the sandstone assemblage of the *Sawdonia ornata* type locality. Facies B is characteristically associated with trimerophytes, especially *Pertica* and *Trimerophyton*, as well as with *Huvenia* and *Sciadophyton*. Of 20 plant occurrences in Facies B, seven are of trimerophytes, four of *Huvenia*, four of *Crenatacaulis*, three of *Sciadophyton*, and one each of *Sawdonia* and *Renalia*. Facies C is characterized by *Spongiophyton* and occasional fragments or (rarely) large logs of *Prototaxites*. Dozens of examples of this association have been observed. Recognizable plant material is usually absent from this association, with the exception of the south shore permineralized sandstone assemblage, which contains abundant large-axis fragments of *Psilophyton* and occasional *Gothanophyton* (inferred anatomy of *Pertica*/*Trimerophyton*), along with abundant permineralized *Spongiophyton* and occasional large fragments of *Prototaxites*. There is a correlation between size of *Spongiophyton* and *Prototaxites* fragments and inferred proximity to source sediments: the most complete pieces of *Spongiophyton* and large *Prototaxites* logs occur in the most

proximal sediments. Conversely, these elements are rare and very fragmentary in the mudstone-dominated facies.

Surfaces occupied by autochthonous gametophytes represent potential sites for establishment of stands of sporophytes, thus affording direct observation of microhabitat during this crucial stage of the life cycle. We term such gametophyte-occupied horizons establishment surfaces. *Sciadophyton* characteristically occurs on fine-grained mud drapes of migrating dunes, or in mud-draped troughs between ripple crests (figure 11.7B). The surfaces were likely wet but subaerial, and apparently represent an influx of sediment affording a fresh, unoccupied surface on which to germinate. Sites episodically shifted laterally, so recolonization of portions of the site after partial burial probably occurred frequently. Vegetative dispersal may have been effected by means of small, thin, round to oval structures resembling moss gemmae, which have been found associated with *Sciadophyton* at several localities (see appendix, figure 11.14E). Cover on *Sciadophyton*-bearing surfaces is relatively limited, ranging from 10 percent to 35 percent. New genus B tends to occupy the finest-grained portions of Facies A, on top of weakly developed gley (water-saturated) soils. None of the establishment surfaces display evidence of significant subaerial exposure; mudcracks and burrows, for example, are virtually absent. These gametophyte assemblages are generally monodominant: five out of six well-exposed *Sciadophyton* horizons, and three of four assemblages with

new genus B, are monotypic. Two exceptions to this rule are noted later.

Stand Composition and Patch Size

Each species (or group of species) was tabulated as abundant (greater than approximately 10 percent) or rare (less than approximately 10 percent) in a given assemblage for all plant-bearing horizons (figure 11.8). Trimerophytes were not further subdivided because of the difficulty of distinguishing species. The megaflora of the Cap-aux-Os Member exhibits low equability (i.e., only a few taxa are abundant). Undoubtedly this is due in part to the lumping of trimerophytes, but even were they recognizable and included as individual species, the species distribution would still be skewed toward the left, reflecting the fact that most taxa in this flora are rare. Trimerophytes as a group are abundant at the largest number of sites; however, zosterophylls tabulated as a group (excluding *Renalia*) are common in nearly as many sites (figure 11.8). Among the zosterophylls, only *Sawdonia ornata* is abundant at a number of sites, whereas the rest tend to be uncommon, or at low abundance, in a given site (figure 11.8). The fact that species distribution at low abundance in a given site roughly mirrors that at high abun-

dance suggests that there is indeed no significant difference in preservation potential among the known fossil megaflora.

Most of the assemblages judged to be autochthonous or parautochthonous on sedimentological grounds are dominated by one taxon, commonly with minor fragmentary components of one or more additional taxa, the latter probably transported elements. However, a few *in situ* assemblages with more than one taxon have been noted. At one site, *Sciadophyton* co-occurs with new genus B, and at another site it intermingles with new genus A, a thalloid plant (see appendix, figure 11.12B). Assemblages that on sedimentary grounds appear to be allochthonous consist of axis fragments and may contain two to eight recognizable taxa in varying abundance. No correlation between taxonomic composition of transported assemblages and sedimentological or inferred paleoenvironmental differences was detected.

The lateral extent of autochthonous assemblages is hard to assess within the measured section because of the steep dip of beds, but several stands of zosterophylls appear to be quite large. For example, the autochthonous *Sawdonia ornata* bed at its type locality extends at least 25 m laterally up to the top of the cliff. The new zosterophyll genus E also forms a distinctive bed that extends at least 30 m up the cliff. Furthermore, this bed is exposed at two sites along the beach that are about 800 meters apart, suggesting a very extensive stand if the bed is in fact continuous. Similarly extensive trimerophyte stands have not been observed.

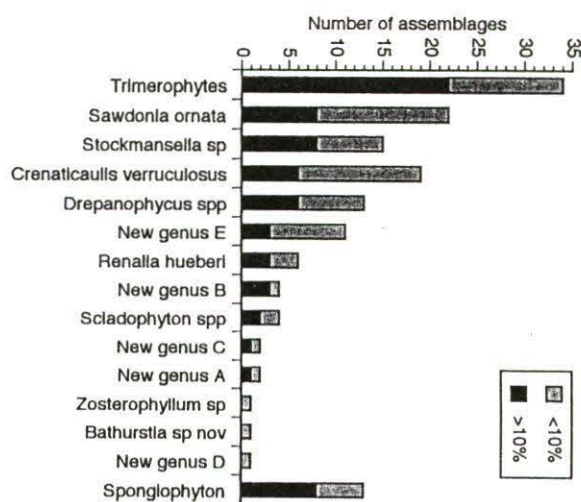


Figure 11.8.

Distribution of megafossil taxa by assemblage (black, abundant in a given assemblage; gray, less than approximately 10 percent in a given assemblage).

In Situ Spores and the Dispersed Spore Record

Although the parent plants of very few species of Devonian *spora dispersa* are known, the converse (that the spores of very few megafossils are known) does not also hold true. Thirteen of 16 species described from the Cap-aux-Os Member have been at least tentatively matched with spores, either from published literature or in the course of this study (see table 11.1). Only one sporangium with spores has so far been

recovered from *Huvenia* sp. nov. These spores, possibly immature or abortive, are smooth and apparently thin-walled, with hints of *curvaturae perfectae* (see appendix, figure 11.14C,D). Spores of *Zosterophyllum* sp. (see appendix, figure 11.15D) and *Crenaticaulis verruculosus* (see appendix, figures 11.15E, 16A,B) are both smooth, with scattered, irregular gemmae, *curvaturae perfectae*, and a darkened patch of exine surrounding the central trilete aperture. Both can be compared to *Retusotriletes rotundus* and similar species. No fertile axes of new genus E have been found, but associated spore masses recovered from a monodominant assemblage of that taxon are also ascribable to species of *Retusotriletes*, such as *R. simplex* (see appendix, figure 11.16E,F). A few spores have been recovered from specimens closely resembling *Drepanophycus spinaeformis* from New Brunswick; these spores are smooth, trilete, and covered with irregular gemmae (Li et al. 2000). All species of trimerophyte collected from the Cap-aux-Os Member, including specimens from the inferred type locality of *Trimerophyton* (*Psilophyton*) *robustius*, have yielded spores referable to the *Apiculiretusispora arenorugosa* morphon (McGregor and Playford 1992). This species complex displays relatively uniform ultrastructure at the SEM level, with a variably attached exoexine comprising an irregular reticulum topped by biform or multiform elements (see appendix, figure 11.17C,D).

The dispersed spore record of the Cap-aux-Os Member displays much greater diversity in both species and morphotype compared to the megafossil record. McGregor (1977) reports 53 species from within the Cap-aux-Os Member. However, direct comparisons of dispersed spore and megafossil species are misleading, because dispersed spore taxonomy is notoriously inflated by reliance on variable, often taphonomically induced characters. A more reliable measure of diversity is number of distinct morphotypes, defined as distinct morphological forms that display little or no intergradation. By this measure, at least 25 distinct morphotypes, in addition to the *Retusotriletes/Calamospora* and *Apiculiretusispora* forms, are recognizable in the

Cap-aux-Os Member (Hotton, unpublished data). With few exceptions, these forms exhibit a pattern of sporadic abundance or are very rare throughout. In contrast, the *Apiculiretusispora* complex comprises from 50 to 99 percent of a given sample, and species of *Retusotriletes* make up from 5 to 20 percent of a given sample, both forms displaying a high degree of constancy from sample to sample (Hotton, unpublished data).

Acritarchs comprise a small but environmentally important component of the Cap-aux-Os Member palynoflora. Approximately 10 species have been identified, including species of *Verruciferum*, *Helosphaeridium*, *Micrhystridium*, *Multiplicisphaeridium*, and *Gorgonosphaeridium*. Most acritarchs are thought to represent cysts of marine phytoplankton (Strother 1997); recent geochemical analyses suggest that many may represent dinoflagellates (Moldowan and Talyzina 1998). They are absent from horizons with autochthonous or parautochthonous plant fossils, but they are moderately abundant in horizons with marine indicators such as brachiopods (e.g., figure 11.3, 21.5 m). Acritarch species diversity is characteristically low in a given horizon within the Cap-aux-Os Member.

DISCUSSION

Niche-Partitioning and Life History Strategies

Sedimentological evidence suggests that plants within the Cap-aux-Os Member displayed incipient niche-partitioning along clade divisions (phyletic niche specialization of DiMichele and Phillips 1996). Many zosterophylls, including *Renalia*, preferentially occupy fine-grained, dysaerobic facies (also noted by Gensel 1986), characteristic of low-energy, water-saturated habitats such as marshes and backswamps (figure 11.9). In some cases, these environments display some organic accumulations. Trimerophytes, *Huvenia*, and *Sciadophyton* preferentially occupy coarser-grained facies suggestive of higher energy, more ephemeral habitats, such as upper bar deposits and cross-bar channels.



Figure 11.9.

Landscape reconstruction of Facies A. Swampy flood basins are covered with monotaxic stands of zosterophylls (e.g., *Sawdonia ornata*). Plant density and branching are illustrated as sparser than the likely actual habit, to demonstrate patterns of vegetative propagation and burial. A flood event (*in background*) initially buried plants with silts and fine sands (distal crevasse-splay deposits), followed by coarser sands containing large fragments of channel-bar and nearbank plants (proximal crevasse-splay deposits). Partially buried plants recovered and continued growing between flood episodes. See text for further details. Drawing by D. H. Griffing.

The occurrence of trimerophytes in the coarser fractions of Facies A suggests that these plants were growing near channel margins and were transported into the flood basin during flood events (figure 11.10).

The Seal Rock area represents a cross section of fluvial environments, with outcrops east of Seal Rock (SRL) representing backswamps, Seal Rock itself representing a channel, and exposures west of Seal Rock (FCW) representing near-channel overbank environments. Plants are distributed systematically among these environments. Large trimerophytes are most abun-

dant in channel and channel margin sediments at Seal Rock. Here also occurs the highest diversity of plants in the Cap-aux-Os Member, where a variety of transported, autochthonous, and parautochthonous plants occur in localized lenses within the channel complex. Trimerophytes, *Huvenia*, and *Sciadophyton*, along with *Crenatacaulis*, are prevalent west of Seal Rock channel in strata that represent habitats slightly farther from the channel margin. Those sites representing backswamps at Seal Rock Landing are dominated by *Crenatacaulis*, *Psilophyton forbesii*, and *Sawdonia*.

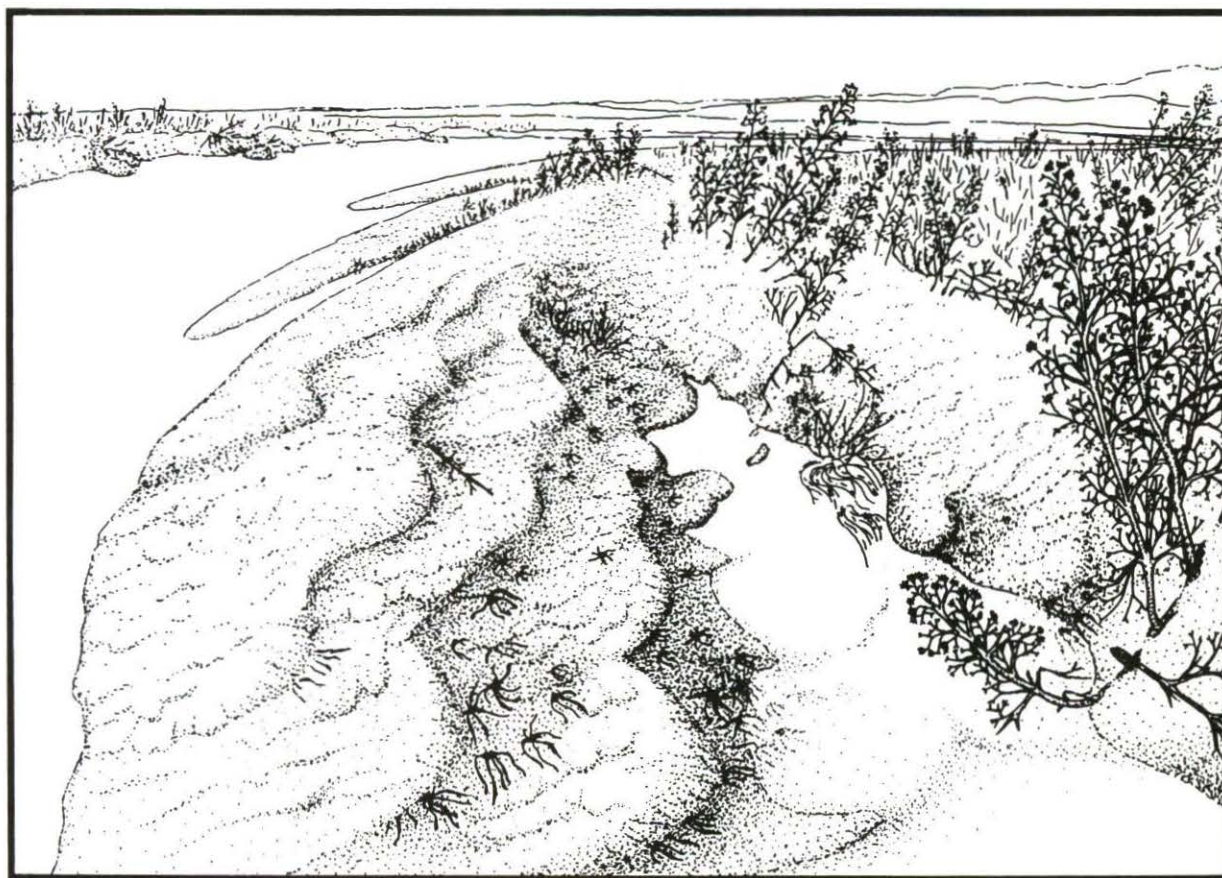


Figure 11.10.

Landscape reconstruction of Facies B. Habitat illustrated consists of point bar along a delta distributary channel influenced only rarely by storm tidal transport. *Sciadophyton* occupies mud drapes in the swales of small dunes within a cross-bar channel (*center foreground*) between flooding events. Episodic floods reorient free axes in downcurrent direction and bury plants in dune sands. Higher portions of the point bar and banks are inhabited by large trimerophytes (*right foreground*), which are toppled and buried by rippled and sheet sands in episodic floods. See text for further details. Drawing by D. H. Griffing.

Niche partitioning correlates with clade-level differences in inferred life history strategies and in morphology. Zosterophylls, although common overall, rarely occur in a fertile state within the Cap-aux-Os Member. Overall, only 5 out of 60 sites contain *any* fertile zosterophylls, excluding *Renalia* (figure 11.11). If numbers of fertile axes are counted, this disparity is increased by orders of magnitude. For example, in the laterally extensive stand of *Sawdonia ornata* at the type locality, only a handful of specimens have been found with sporangia. Given their low sporangial production, most of these zosterophylls were probably in a vegetative state for most of their life cycle. Furthermore, many zosterophylls retained the capacity to continue vegetative growth after

sporangial production. The characteristic lateral and terminal circinate buds of zosterophylls suggest a stored potential for extensive vegetative growth within the constraints of a determinate growth system, which in turn suggests both dependence on vegetative growth to establish large stands and a capacity to remain in a site over an extended interval. That zosterophylls sometimes formed extensive stands is further evidence of their capacity for extended vegetative growth. The types of environments that zosterophylls preferentially occupied appear to have been sufficiently stable to allow some accumulations of organic matter. In addition, the xeromorphic aspect of their cuticle (tough, thick cuticle, sunken stomata) likely reflects oligotrophic

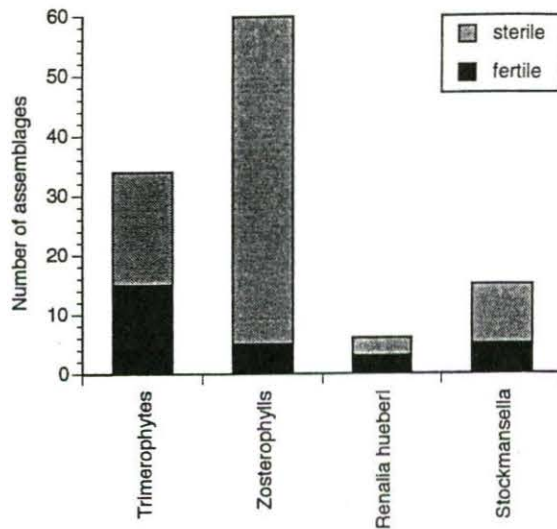


Figure 11.11.

Presence of fertile and sterile specimens in a given megafloral assemblage, by major taxonomic group (black, fertile; gray, sterile). A single fertile specimen in a given assemblage is sufficient to be included in the fertile category.

conditions in dysaerobic, water-saturated habitats, rather than xeric conditions.

In contrast, the morphology of trimerophytes suggests a more opportunistic and ephemeral life history strategy. Trimerophytes commonly occur in a fertile state, with about 45 percent of the assemblages containing at least some fertile axes (figure 11.11), suggesting that a significant part of their life cycle was spent in a fertile state. This in turn suggests that they grew rapidly and achieved reproductive maturity quickly. Their thin cuticle, which displays poor resistance to chemical oxidation in contrast to zosterophylls, is also consistent with rapid growth (although many other factors also influence cuticle thickness). The terminal sporangia of trimerophytes, in which apical meristems were apparently converted to fertile structures, suggests that aerial shoots at least were monocarpic. For example, in complete specimens of axes from the presumed *Trimerophyton robustius* type locality, both terminal apex and lateral branches terminate in a corymb-like arrangement of sporangia, all apparently at an equal stage of maturity (see appendix, figure 11.17B). It appears likely that the aerial shoots of trimerophytes completed their life cycle with a burst of reproduction, although they may have been produced season-

ally from a perennial rhizome. Rapid growth and abundant sporangial production would have been a selective advantage in the kinds of ephemeral environments that trimerophytes occupied. Sedimentological evidence also supports the inference of rapid development: Surfaces on which these plants apparently were anchored display evidence of reactivation during floods, suggesting that these plants may have had to complete their life cycle within a short time, perhaps as little as a few months. Although it may appear paradoxical that the tallest early land plants were fast growing and short-lived, the main selective force for height may have been to broadcast spores into the air stream, rather than for light interception (Tiffney 1981).

Not all plants of the Cap-aux-Os Member follow this simple model. *Renalia* occurs in the same kind of low-energy environments as zosterophylls, but it is comparable to trimerophytes in the frequency with which it is found fertile (figure 11.9). However, in other respects, it resembles zosterophylls in bearing sporangia laterally (on small lateral branches), and in possessing elongated axes with numerous "branch buds" suggestive of a clambering habit. *Huvenia* sp. occupies higher-energy environments and displays moderate levels of fertility (figure 11.11), but it bears sporangia on small lateral branch spurs; thus at least the potential for continued growth after spore production remains. *Crenaticaulis verruculosus*, a zosterophyll, characteristically occurs in Facies B; however, it tends to occupy the quiet water portions of upper bar environments.

Zosterophylls and trimerophytes occupy two of the three vertices in the life history model of Grime (1977). Zosterophylls fit the model of stress, or S-selected, species, occupying physiologically stressful habitats (for example, dysaerobic or nutrient-poor sites), whereas trimerophytes are ruderal, or R-selected, species, occupying sites subject to high levels of disturbance and displaying high reproductive output and an inferred short life span. Ruderal selection, suggested by the small size and terminal sporangia of the earliest polysporangiophytes, may well represent the ancestral embryophyte life history

strategy (Niklas et al. 1980; Gray 1984). In contrast, stress selection may be a somewhat later development, involving acquisition of physiological and morphological traits for extended site occupation and resource acquisition (Beerbower 1985). Certain zosterophyll characters, such as resistant cuticle, continued growth of the axis after sporangial formation, and copious production of branch buds, may be interpreted as adaptations toward stress tolerance. These traits may, in fact, represent adaptations to hydric habitats, which sedimentological evidence suggests may have evolved very early within the lycophyte clade.

The dispersed spore record might be expected to mirror the megafloral pattern, but preliminary cluster and principal components analyses of the palynoflora have yet to reveal a clear pattern. This is probably because trimerophyte spores swamp practically every other form in almost all samples. Many of the dispersed *Retusotriletes* type spores probably also represent the inner bodies of *Apiculiretusispora*, since only a small fraction of dispersed *Retusotriletes* species closely resemble *in situ* zosterophyll forms. Variation probably occurred on a very small scale (meters to tens of meters), due to the low stature of the plants, and any consistent pattern is likely erased through transport. Likewise, transported megafloral assemblages display purely random variation, probably for the same reason.

Monodominant Assemblages

Megafloral data from this study reaffirm observations by many others that early land plants tended to form monodominant stands (Bateman 1991; DiMichele et al. 1992). Furthermore, some evidence from *in situ* gametophytes (primarily *Sciadophyton*) suggests that monodominance begins at the gametophyte stage; however, the sample is too limited to rule out the possibility of inter gametophyte competition resulting in sporophyte dominance (Edwards and Davies 1990). In any case, the tendency toward monodominance in early land plants is not a necessary attribute of "primitive" embryophytes, as witness the mixed species assemblages

of modern moss microcommunities. Several factors could be controlling establishment in early land plants. For example, rapid clonal growth from a single or limited number of spore germination events may characterize the type *Sawdonia* locality, whereas rapid reoccupation of partially covered stands appears to occur at many of the Seal Rock localities, where successive horizons are filled with the same plants. In both cases, rapid mat-forming growth that excludes other species is the mechanism that results in monotypic patches. However, extreme patchiness of available habitats, rendering occupation by more than one species at a time unlikely, may also have been a factor, although probably less by the late Emsian. Monotypic assemblages, especially clones where the plants are genetic copies of one another, would presumably have experienced little intra- and inter-specific competition (Tiffney and Niklas 1985; DiMichele et al. 1992). Despite this, land plants had by Emsian times apparently begun to divide the landscape, whether driven by chance or by competition at the margins of patches.

Coastal versus Fluvial Habitats

At first glance, the absence of embryophyte fossils and the predominance of *Spongiophyton* and *Prototaxites* in large fluvial channels appear to support the view that early land plants were restricted to coastal environments, with *Spongiophyton* and *Prototaxites* forming a transported assemblage from near-channel sites upstream. However, limited evidence from a few channel palynoflorules, as well as the south shore permineralized sandstone assemblage, suggests the presence of at least some tracheophytes in fully fluvial environments upstream, notably *Psilophyton* and other trimerophytes. Several reasons for the apparent rarity of embryophytes from such environments may be adduced. It is possible that they were in fact rare and patchily distributed on the landscape, therefore rarely preserved. However, we think it more likely that fluvial environments were much less conducive to plant preservation, as a result of such factors as high oxidation levels, and especially to the

susceptibility of herbaceous plants to fragmentation under the high-energy regime in which these channels were deposited.

The sedimentological context of *Spongiophyton* and *Prototaxites* alone, regardless of their taxonomic affinities, unequivocally establishes them as terrestrial organisms with a marked preference for fully fluvial, rather than coastal, environments. Thick lenses of *Spongiophyton* on channel dunes suggest that it was growing in abundance along the channel margin. The fact that the larger fragments of *Prototaxites* occur in more proximal channels also strongly suggests that it was growing in far-inland sites and was occasionally rafted downstream into more coastal environments. The *Spongiophyton*/*Prototaxites* assemblage is puzzling not for its occurrence in fluvial channels but for its absence from plant-rich coastal environments. If these organisms were fungi, one might expect that they would find such nutrient-rich habitats congenial. Hypotheses for their absence may be proposed: For example, they may have been unable to tolerate salinity fluctuations or have been unable to occupy the muddy, shifting surfaces of tidal flats and backswamps. *Prototaxites* was capable of attaining immense size, suggesting a life cycle measured in years rather than months; perhaps it occupied more stable environments such as the edges of large, inland lakes. However, such possibilities remain speculation until the life habitats of this organism are characterized.

Occupation of High-Stress Environments

Were early land plants restricted to moist, mesic habitats? Sedimentological evidence points to occupation by both sporophytes and gametophytes of fine-grained, water-saturated substrates. The need for water by gametophytes is a given, and indeed is often cited as the reason for restriction of early land plants to such environments. There is some reason to believe that this may not have been insuperable. For example, the occurrence of cuticle, stomata, and a rudimentary conducting system in *Sciadophyton* suggests that it was much more tolerant of water stress than free-living gametophytes of modern

plants; the same may have been true of other early land-plant gametophytes as well. Nevertheless, fine-grained substrates and at least ephemeral water availability was almost certainly a requirement for establishment of gametophytes, if not for long-term occupation by sporophytes. Many zosterophylls apparently preferentially occupied moist, fine-grained substrates, and sites occupied by trimerophytes seem to have been only marginally less wet and more energetic. However, the limitations of sedimentary evidence must be kept in mind: Wet, dysaerobic environments are precisely the sites where fossils are likely to be preserved, whereas xeric sites are generally poor prospects for preservation. Evidence of occupation of more xeric sites comes from indirect evidence such as root traces. Millimeter-wide, obliquely directed traces that dichotomize downward occur in some of the more oxidized paleosols of the Cap-aux-Os Member (see also Elick et al. 1998a; see chapter 13), suggesting that at least some plants could occupy more xeric sites. However, strong taphonomic bias toward preservation of water-saturated environments remains a serious obstacle to fully characterizing early land plant habitats. More data, especially from paleosols where trace evidence of root and rhizome activity is preserved, are needed before we can draw conclusions about the capacity of early land plants to occupy xeric habitats.

Good records exist for one type of stressful environment in the Cap-aux-Os Member, namely brackish and saline habitats. Salt tolerance is a derived trait among embryophytes, requiring physiological and morphological modifications, and it is especially rare among bryophytes and pteridophytes (Schuster 1966; Brown 1983). Thus, we might expect early land plants to occupy primarily or exclusively freshwater sites. Within the limits of resolution, this appears to be the case for plants of the Cap-aux-Os Member. Autochthonous and parautochthonous assemblages of both sporophytes and gametophytes occur in sites lacking clear marine fossil and sedimentological indicators. Conversely, only plant fragments occur in clearly tidal or marine facies. Acritarchs, the most sensitive indicator

of salinity within our study area, are absent or very rare from autochthonous and parautochthonous plant horizons, although they are moderately abundant in brachiopod horizons (figure 11.3). Even in clearly marine horizons within the Cap-aux-Os Member, acritarch diversity is low, which is especially characteristic of nearshore marine habitats (Staplin 1961; Wicander and Wood 1997 and references therein). These data do not preclude the possibility that plants were at times exposed to brackish conditions, especially given that they occupied tidally influenced environments that would have been subjected to periodic inundation from the sea. Equivalent modern environments represent a mosaic of brackish and freshwater habitats that may be separated at a meter-level scale. It is difficult to determine from the sedimentological record whether plants tolerated occasional inundation of brackish or saline water, or were killed by them. However, there is no evidence that any species preferentially or consistently occupied identifiably brackish habitats, and indirect evidence suggests that they did not grow in such environments. This suggests that members of the Cap-aux-Os flora, at least, had not acquired the types of physiological and morphological adaptations necessary for occupation of saline habitats (see also Edwards 1980).

Apparent versus Actual Floral Diversity

The megafossil evidence implies a low-diversity flora of simple structure, dominated by a few common and many rare species that formed monodominant stands of limited extent and probably limited interaction. The megaflores and palynoflora both suggest that the Cap-aux-Os flora was of low equability (i.e., it was dominated by a few common taxa with a high percentage of taxa characterized by few or single occurrences). Although this pattern may approximate the true species distribution, it must be kept in mind that the megafossil record is biased in a number of ways; thus, intrinsic properties of the dominant clades may tend to overestimate their actual importance on the landscape. For example, trimerophytes appear

overwhelmingly dominant; however, their high spore productivity and their occupation of near-channel habitats may overestimate their actual abundance on the landscape. Likewise, many zosterophylls tend to occupy wetland sites likely to be preserved, and thus they may be overrepresented in the fossil record relative to their true abundance.

That the megafossil record is biased certainly comes as no surprise, given that numerous modern taphonomic studies have established the propensity toward preservation of plants growing near sites of deposition (Spicer 1989). However, the dispersed spore record suggests that the early land plant megafossil record is particularly deficient in capturing actual floral diversity. Comparison of *in situ* spores and *spores dispersae* of the Cap-Aux-Os Member shows that the two dominant megafossil clades, trimerophytes and lycophytes, account for only a small fraction of the morphological diversity of the *spores dispersae*. In this respect, the Cap-aux-Os flora mirrors the disjunction observed from many other localities of similar age (Gray 1984, 1993; Fanning, Richardson, and Edwards 1991; Edwards 1980, 1996), and it pinpoints a central problem in Devonian plant paleoecology. The diversity of the dispersed spore record strongly suggests that many forms, perhaps whole classes of plants, have thus far escaped sampling in the megafossil record. Some of the rarest unknown morphotypes may be derived from extrabasinal plants (Allen 1980; Gray 1984). However, many unknown spore types are sporadically abundant at individual horizons, suggesting that they occupied the same coastal fluvial environments as the megafossils (although probably drawn from a wider range of environments that includes habitats unsuitable for megafossil preservation). The parent plants of many of these unknowns may be of bryophytic grade (Richardson 1985; Edwards 1996). Their apparent absence in the mega-fossil record could be attributable to low preservation potential; however, another cause could be their very small size, which renders them easily overlooked. The discovery of small forms in the Cap-aux-Os flora through bulk

maceration, such as new genus C, lends support to the latter explanation. The rarity of the dispersed spore morphotypes could be due to any of a number of factors. The parent plants might sexually reproduce rarely or produce fewer spores, or they may be short statured, so that their spores do not disperse widely, or they may be ephemeral, or rare and patchily distributed on the landscape. In any case, the apparently simple Early Devonian landscape was likely more diverse, with more complex kinds of interactions, than may be inferred from the megafossil record alone.

CONCLUSIONS

The Cap-aux-Os Member of the Battery Point Formation was deposited within a low-lying fluvial-deltaic coastal plain. Plant megafossils are restricted to a relatively limited number of wet environments. Indirect evidence suggests that plants probably occupied primarily or exclusively freshwater habitats. Autochthonous and parautochthonous assemblages of both sporophytes and gametophytes were for the most part dominated by one species, suggesting limited interspecific competition among early land plants. Nonetheless, sedimentological evidence supports an inference of clade-related niche-partitioning; many zosterophylls appear to have preferentially occupied dysaerobic, wetland sites within intertributary basins, whereas trimerophytes and rhyniopsids apparently occupied more ephemeral, near-channel environments. Both sedimentological and morphological evidence suggest a stress (S-) selected life history strategy for zosterophylls, in contrast to ruderal (R-) or disturbance selection in trimerophytes. These observations are based on a small sample of plants from a limited geographic area and time interval. They provide sufficient data to frame hypotheses; whether these hypotheses hold true requires comparably detailed sedimentological analyses of other early land plant localities.

At least certain early land plants, notably trimerophytes, as well as the probably eumyce-

tous *Spongiophyton* and *Prototaxites*, occupied fully fluvial (riparian) environments, but the plant fossil record remains heavily biased toward low-lying coastal communities. The extent of plant cover at this time remains a difficult question to address. Nevertheless, we think it unlikely that early land plants were restricted to moist mesic sites by their free-sporing life cycle (Algeo and Scheckler 1998). Certainly many extant bryophytes and pteridophytes occupy extremely hostile habitats such as bare rock substrates, and hot and boreal deserts; bryophytes in particular are common in pioneer habitats. The need for moisture for germination and fertilization in free-sporing plants is short-lived, and sexual reproduction need take place only rarely as long as vegetative means of propagation are available. Extant free-sporing plants adapt to harsh conditions in a variety of ways, through rapid completion of the life cycle, physiological resistance to desiccation, dormancy, or reduced resource allocation (Gray 1985). Early land plants faced an environment that was at least as hostile as any modern landscape, without soil or plant cover other than algal and bacterial mats. It would be surprising if they had not developed extensive physiological and morphological adaptations to harsh conditions that would enable them to cover a large portion of Earth's surface by Emsian times.

The dispersed spore record reminds us that embryophyte diversity, and consequently ecosystem complexity, was likely much higher than is reflected in the megafossil record, a point made forcefully by Gray (1985). Furthermore, the rarity of many of these morphotypes does not necessarily signify that their parent plants were rare; even if their reproductive output was low, they may yet have been important players on the landscape. We emphasize the apparent bias of the megafossil record not as a counsel of despair but rather as a call to action. Continued search, especially through bulk maceration of fine-grained sediments (Edwards 1996), and ultrastructural study of dispersed fossil spores are just two potentially fruitful approaches to close the gap between the mega- and palynofloral record.

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Appendix

Descriptions of Plant Megafossils

Brief descriptions of new taxa as yet unpublished, as well as our perhaps idiosyncratic treatment of certain existing taxa, are presented here. This list is not to be considered a formal taxonomic treatment. Taxa that appear to us to be well founded and well described in the literature are not discussed. Classification of major clades follows Kenrick and Crane (1997a). All figured and type specimens are to be deposited in the National Type Collection, Ottawa, Canada.

EMBRYOPHYTYA INCERTAE SEDIS

New Genus A

The material consists of elliptical, dichotomously lobed, thalloid structures roughly 2–3 cm × 3–5 cm (figure 11.12B), with little cellular detail visible. In gross morphology it resembles a thalloid liverwort such as *Marchantia*.

New Genus B

Specimens are cespitose, consisting of isotomously branched axes about 1 mm wide, terminated by paired reniform “cups” (figure 11.12A,C). Each cup bears scattered small, round, or oval structures on short stalks (figure 11.12D,E), which may be antheridia. This taxon is under study by F. M. Hueber and C. L. Hotton; similar plants, but lacking the paired cups, have been illustrated by Remy et al. (1993) and are under study by P. Gensel and associates.

New Genus C

Only distal portions of the plant, bearing sporangial trusses, have been recovered. Sporangia are borne in a cymose fashion—that is, each sporangium terminates a branch, which undergoes two close dichotomies subterminally to give rise to another sporangium, and so on (figure 11.13A). Axes display no evidence of conducting tissue. Sporangia range from 0.2–0.5 mm wide and 0.5–1.5 mm long; they narrow to a thickened pore at the apex and display no evidence of a dehiscence structure (figure 11.13B). This plant may represent a new major clade of polysporangiophyte, or alternatively it could represent a primitive moss or hepatic (Hotton and Newton, unpublished data).

RHYNIOPSIDA

New genus D

(“*Taeniocrada dubia*” Hueber 1983)

This plant consists of broad strap-shaped axes 0.9–2.0 cm wide, with thin but resistant cuticle, often unbranched, or anisotomously or rarely isotomously branched (figure 11.13C). The surface is covered with conspicuous oval stomata. Larger oval scars consisting of a raised ring surrounding a depression and a central papilla, approximately 1–1.4 mm wide by 1.5–2.0 mm long, occur on some axes [“areoles” of Dawson (1871)] (figure 11.13F). We interpret these larger scars as sporangial attachment scars

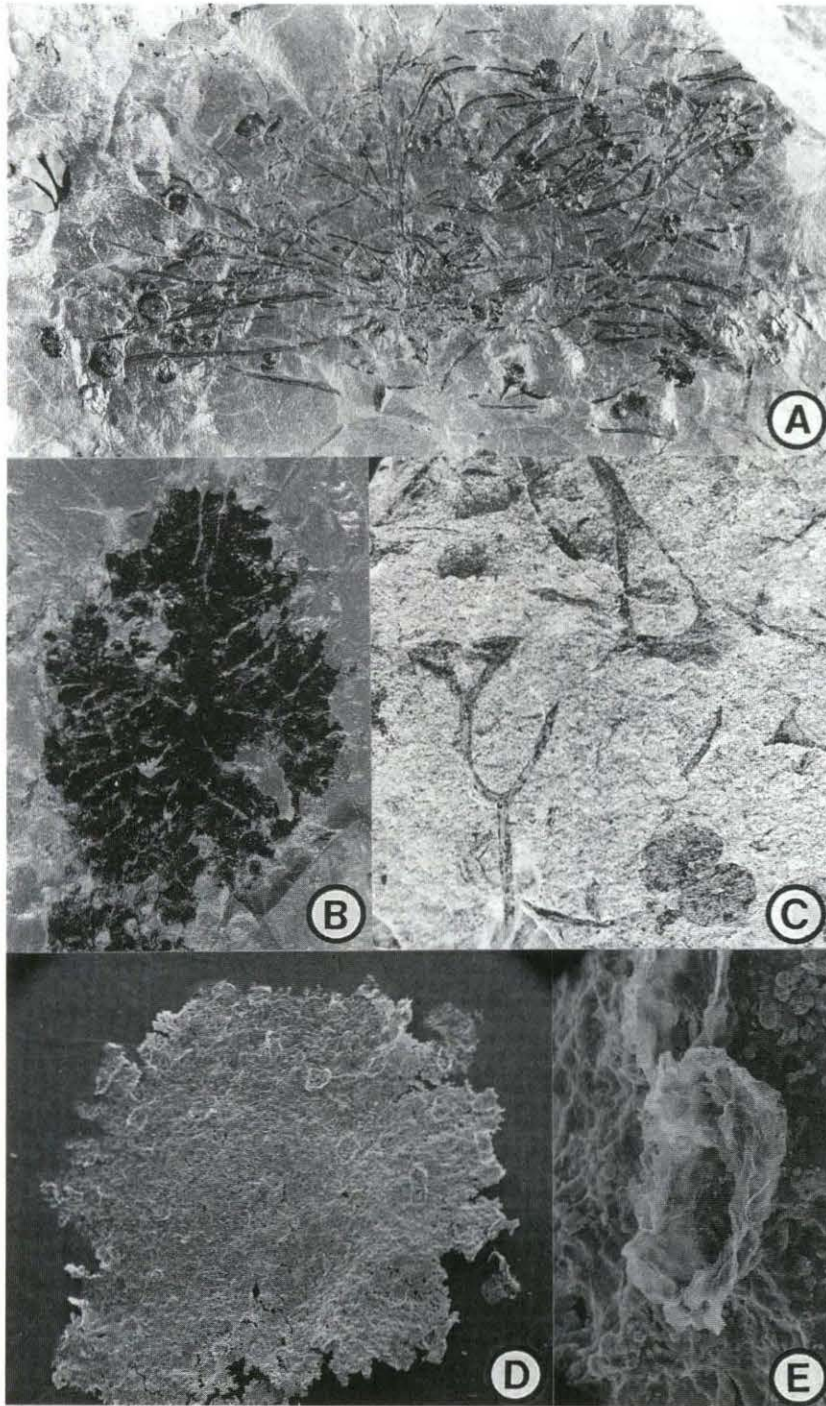


Figure 11.12.

A: New genus B. Probable gametophyte. Cap-aux-Os Member, Association 2. Compression of whole plant. Note cespitose habit and terminal "cups". DAA95-P7. $\times 0.6$. **B:** New genus A. Compression of possible hepatic. Cap-aux-Os Member, Association 2, DAA95-P7. $\times 1.2$. **C:** New genus B. Compression/impressions of terminal cups. Note plan view of paired cups and lateral view of another specimen perpendicular to bedding plane. FMH 1967. $\times 0.6$. **D:** New genus B. Upper surface of cup (SEM). Note scattered bowl-shaped structures on short stalks on surface, interpreted as possible antheridia. FMH 1967. $\times 15$. **E:** New genus B. Detail of stalked structure (= ?antheridium) from another cup (SEM). FMH 1967. $\times 180$.

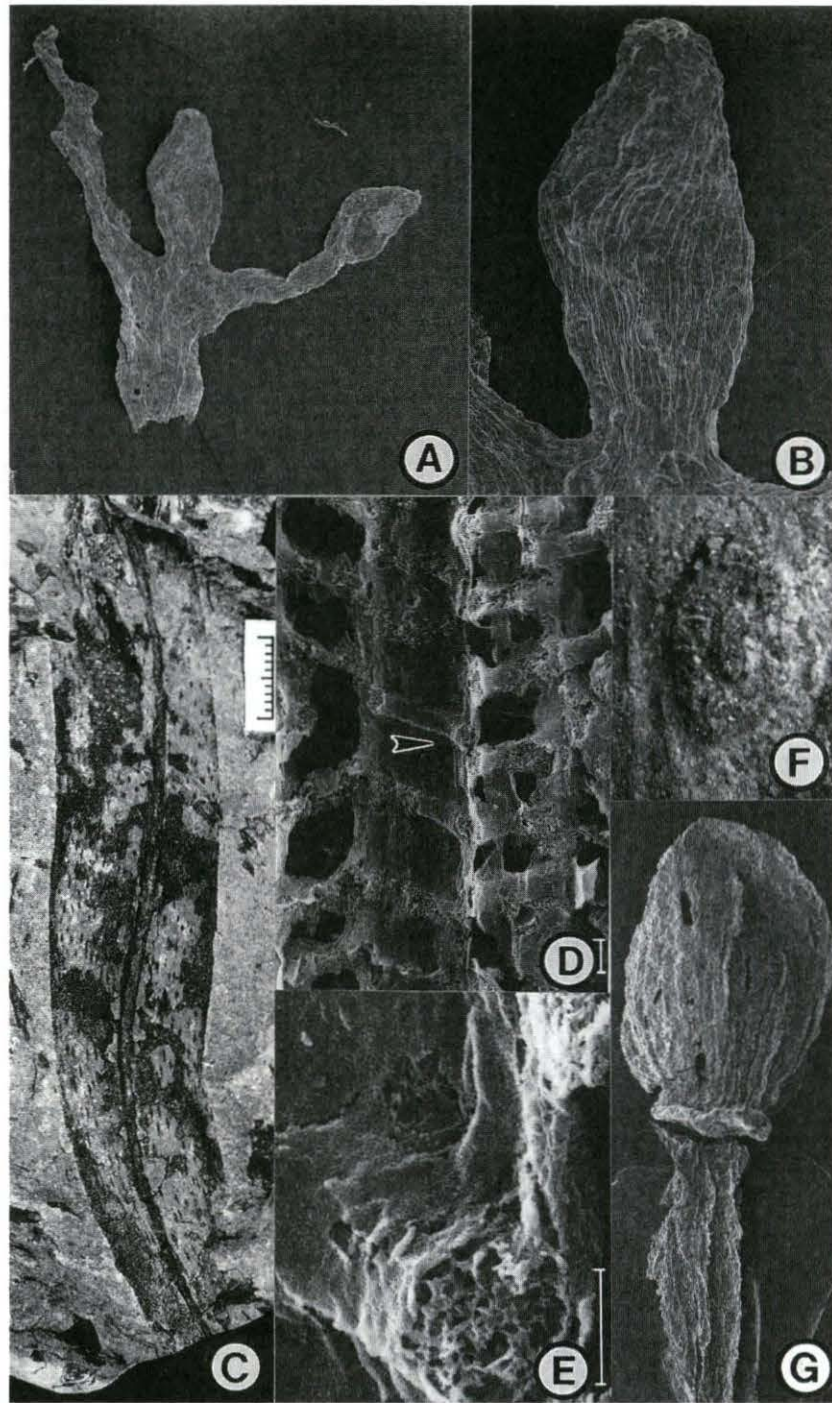


Figure 11.13.

A: New genus C (*Embryophyta incertae sedis*). Cap-aux-Os Member, Association 2, DAA95-P15. Distal sporangial truss, displaying "cymose" habit (SEM). $\times 60$. **B:** New genus C. Detail of central sporangium. Note apical knob with apparent pore (SEM). $\times 60$ (B). **C:** New genus D, Rhyniopsida (= "*Taeniocrada dubia*" Hueber 1983). Battery Point Formation, Gaspé Bay. Axis compression with permineralized vascular strand. Note oval pits (stomata). South shore of Gaspé Bay, approximately 1 km NW of axis of Cap Blanc anticline. GSC 6322. Scale, 1 cm. **D:** New genus D. S-type tracheids from specimen in (C). Note change in gyre of thickening on tracheid at left (SEM). $\times 400$. **E:** New genus D. Detail of tracheid

because of their resemblance to such structures in *Huvenia* sp. nov. (compare figures 11.13F and 11.14B). Permineralized axes from the south shore of Gaspé Bay, of the same size and morphology but lacking sporangial attachment scars, have a terete central strand with S-type tracheids (figure 11.13D,E). The anatomy and attachment scars are evidence that this plant is a member of the rhyniopsid clade (Kenrick and Crane 1997a). This species is currently under study by F. M. Hueber and C. L. Hotton.

Huvenia sp. nov.

This plant consists of axes about 0.5 cm wide and up to 20 cm long, with distinct longitudinal plications (figure 11.13G). Sporangia are round to ovoid, borne on shortened branchlets, with thickened, radially elongate cells at the base, forming a distinctive scar, or "collar" (figure 11.14A,B). Spore masses clinging to one sporangium (figure 11.14C) are roughly 60 μ m in diameter, smooth, more or less spherical, apparently thin-walled, and trilete, with hints of *curvaturae imperfectae* (figure 11.14D). This species is currently under investigation by P. Gensel and students.

Small, round to oval discs (figure 11.14E), sometimes paired, have been found closely associated with, and possibly attached to, axes of *Sciadophyton* sp. We hypothesize that these functioned as vegetative disseminules of these plants.

ZOSTEROPHYLLOPSIDA

"*Bathurstia*" sp. (New Genus F)

Two specimens were recovered from the Seal Rock area that are identical to plants under

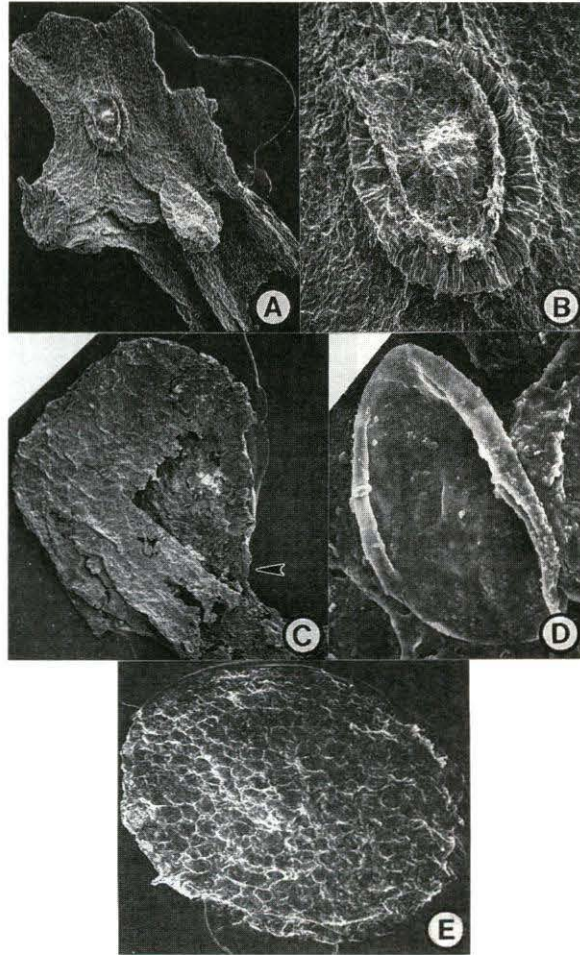


Figure 11.14.

A: *Huvenia* sp. nov. Cap-aux-Os Member, Association 1, FCW94-P15. Fragment of axis with sporangial bases borne on very short side branches (SEM). $\times 15$. **B:** *Huvenia* sp. nov. Detail of sporangial base in figure 11.14A; compare with figure 11.13FA (SEM). $\times 47$. **C:** *Huvenia* sp. nov. Sporangium with clumps of spores (SEM). $\times 25$. **D:** *Huvenia* sp. nov. Proximal view of single spore from cluster near base of sporangium in (C) (arrow). Note indistinct trilete aperture and hint of *curvaturae* in upper part of photo (SEM). $\times 694$. **E:** Small, flat disc (gemma-like structure), composed of probably no more than two cell layers, associated with *Sciadophyton* sp. Cap-aux-Os Member, Fort Péninsule, GSC 5411. $\times 70$.

Figure 11.13 (continued)

from (D) (at arrow), showing alveolar internal layer and microporate covering (SEM). $\times 3,000$. **F:** New genus D. Impression of oval scar on another axis: probable site of sporangial attachment. Cap-aux-Os Member, Association 1, Seal Rock area, pyrite sandstone. FMH 1967. $\times 18$. **G:** *Huvenia* sp. nov. Note thickened "collar" of cells at base of sporangium and plicate axis. Cap-aux-Os Member, Association 1, FCW94-P15. $\times 11$.

study from Campbellton, New Brunswick. These consist of isotomously branched axes, 3–6 mm wide, with two rows of short, acicular spines along the margins of otherwise smooth axes. Regions of tightly clustered sporangia are interspersed with vegetative regions (figure 11.15A). No spores have been recovered from any of these specimens. Although these specimens

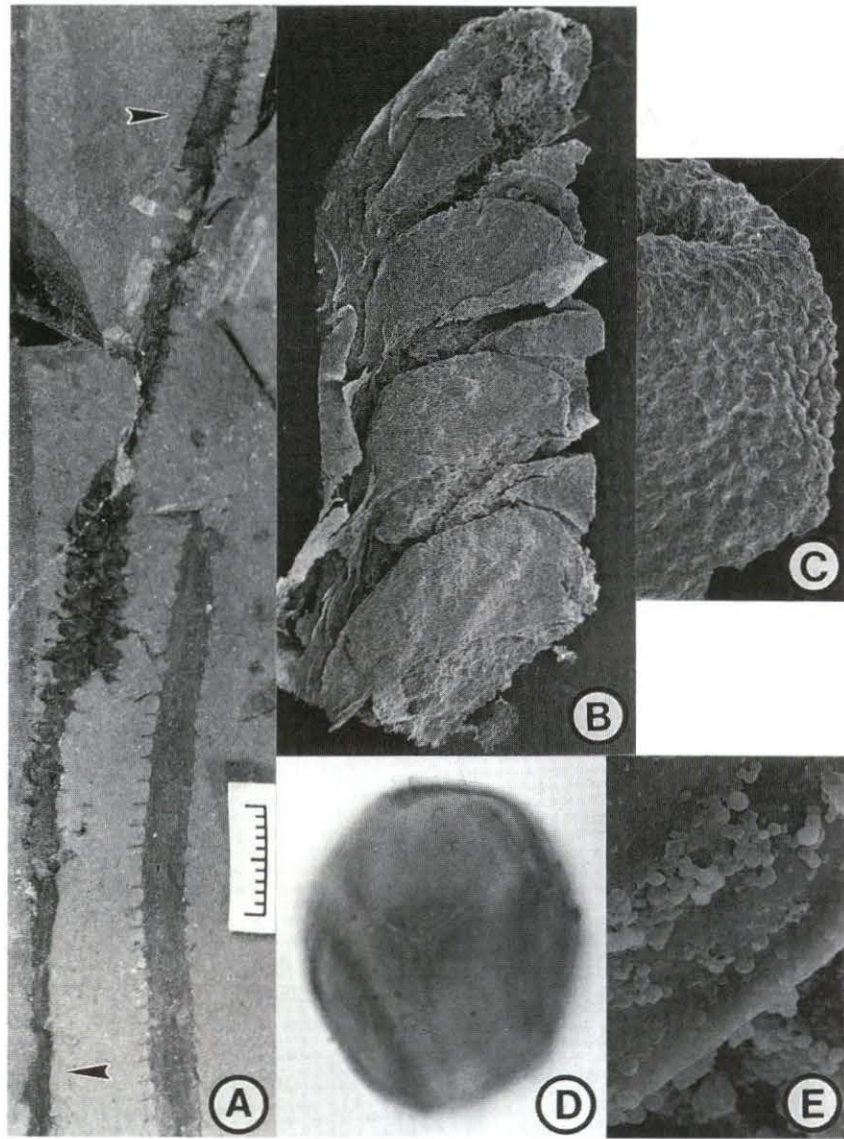


Figure 11.15.

A: "*Bathurstia*" sp. (new genus F) (impression). Note sporangia clustered in central portion of axis with vegetative portions above and below (*arrows*). A second vegetative axis displaying short narrow spines is to the right. Campbellton, New Brunswick. GSC 6267. $\times 1.4$. **B:** *Zosterophyllum* sp. Cap-aux-Os Member, Association 2, 91-3z. Whole spike (SEM). Note alternating, bilateral position of sporangia. $\times 13.5$. **C:** *Zosterophyllum* sp. Detail of central sporangium in (B). Note papillate thickenings on cell surface. $\times 90$. **D:** *Zosterophyllum* sp. Proximal view of one of the spores freed from a sporangium by mechanical means. Note scattered gemmae, curvatural ridge in focus to left, and darkened central patch around trilete aperture. $\times 1,000$. **E:** *Crenaticaulis verruculosus* spore, detail of spore ornamentation. Note irregular gemmae on both spore and sporangial surface (SEM). Compare to (D) and figure 11.16F. $\times 3,500$.

were initially interpreted as a new species of *Bathurstia*, recent work by Kotyk (1997) has shown substantial differences in vegetative and reproductive morphology between the type species of *Bathurstia* and these new forms, suggesting that they should be placed in a new genus.

***Zosterophyllum* sp.**

Our material consists of spikes of bilateral, alternating rows of sporangia approximately 2–3 mm wide (figure 11.15B). Tufts of narrow, isotomously branched axes approximately 1.5–2.5 mm wide are closely associated on the same bedding surface but not attached. Sporangia lack clear dehiscence lines, and the cells are distinctly papillate (figure 11.15C). Spores are irregularly gemmate, range from 50 to 100 μm in diameter, and conform to the *Retusotriletes* type, with distinct, narrow *curvaturae* paralleling the equator, and a darkened area surrounding the trilete aperture (figure 11.15D).

***Crenaticaulis verruculosus* Banks and Davis**

A single fertile axis bearing three sporangia with abundant *Retusotriletes*-type spores clinging to the inner sporangial surface (figures 11.15E, 11.16A,B) adds new detail to this well-described species.

New Genus E

Axes are isotomously to anisotomously branched, 0.5–1.2 cm wide (figure 11.16C), some branches ending in circinate buds, with axillary “tubercles” just below each dichotomy (figure 11.16D). The cuticle is extremely tough, with regularly arrayed papillae forming a chevron pattern (figure 11.16D). Although no sporangia have been found attached, the aforementioned vegetative characters clearly place it among the zosterophylls. Reniform spore masses macerated from a monotypic assemblage of the plant are small (30–45 μm in diameter), with *curvaturae perfectae* and irregularly scattered gemmae (figure 11.16E,F). This species is currently under study by P. Gensel and students.

***Eogaspesiea gracilis* Daber**

Extensive collections and maceration of material from the Cap-aux-Os Member have failed to recover any fossil resembling the description of *Eogaspesiea* [i.e., sparsely isotomous, narrow axes bearing single terminal fusiform sporangia (Daber 1960)]. Furthermore, new collections of material from the type locality of *Eogaspesiea gracilis* at Seal Rock have revealed sporangia and vegetative axes closely resembling *Renalia hueberi*. We offer the hypothesis that the original description of *Eogaspesiea* is in error, and that the two genera are similar or perhaps identical.

TRIMEROPHYTES

Plants attributable to this group are instantly recognizable even as fragments on the basis of (1) their paired, fusiform sporangia, often containing spores with an irregularly sloughing, apiculate outer exine, and (2) their rigid, often anisotomously branched axes with elongate epidermal cells, and (3) their thin, chemically unresistant cuticle. Distinguishing among species within this group is much more difficult. Three species of *Psilophyton* have been described from the Battery Point Formation: *P. dawsonii*, with smooth axes (Banks et al. 1975); *P. forbesii*, with ridged axes (Gensel 1979); and *P. princeps*, with stout, possibly glandular emergences capped by a cup-shaped structure (Hueber 1967). Only the first two of these taxa have been recognized in the course of this study.

Two genera of large trimerophytes with erect sporangia are usually recognized: *Trimerophyton*, with “trichotomous” branching (i.e., two close dichotomies) (Hopping 1956); and *Pertica*, with variably opposite-decussate, quadriseriate, or spiral branching (Kasper and Andrews 1972; Granoff et al. 1976; Doran et al. 1978). In our opinion, branching in this group is both far more complex than implied by these terms and highly variable across and within species. For example, exceptionally complete specimens of a large smooth trimerophyte, collected by D. C. McGregor in 1960, display opposite-decussate

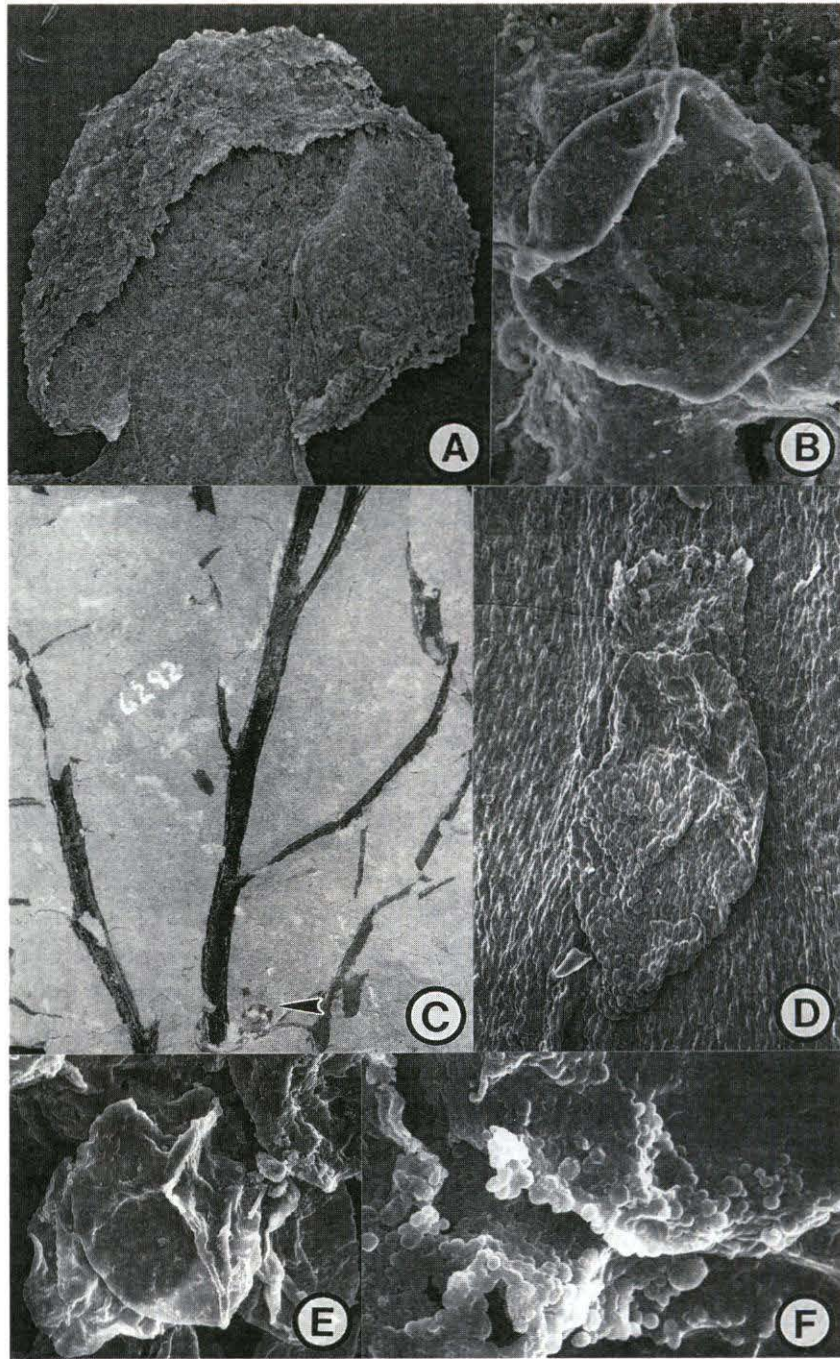


Figure 11.16.

A: *Crenaticaulis verruculosus* sporangium with spores, portion of fertile axis macerated from matrix. Cap-aux-Os Member, Association 1, Seal Rock Landing, SRL93-O17. Whole sporangium (SEM). Note valves of unequal size and papillate cells typical of *C. verruculosus*. $\times 22$. **B:** *Crenaticaulis verruculosus*. Proximal view of *in situ* spore from (A) (SEM). Note curvaturate ridges visible near equator (arrow). $\times 1,000$. **C:** New genus E (zosterophyll). Cap-aux-Os Member, Association 1, Seal Rock. Compressions of axes. Note isotomous branching and circinate bud (arrow). GSC 6292. $\times 0.6$. **D:** New genus E. Axillary tubercle located laterally and just below dichotomizing axis (SEM). Note chevron pattern of papillate cellular thickenings. SRW95-P3. $\times 35$. **E:** Proximal view of spore from spore mass isolated from monotypic assemblage of new genus E (SEM). Note long trilete ridges and hints of *curvaturae perfectae*. SRL93-D. $\times 1,000$. **F:** Detail of ornamentation of several other spores from the spore mass in (E). Note irregular gemmae. $\times 3,300$.

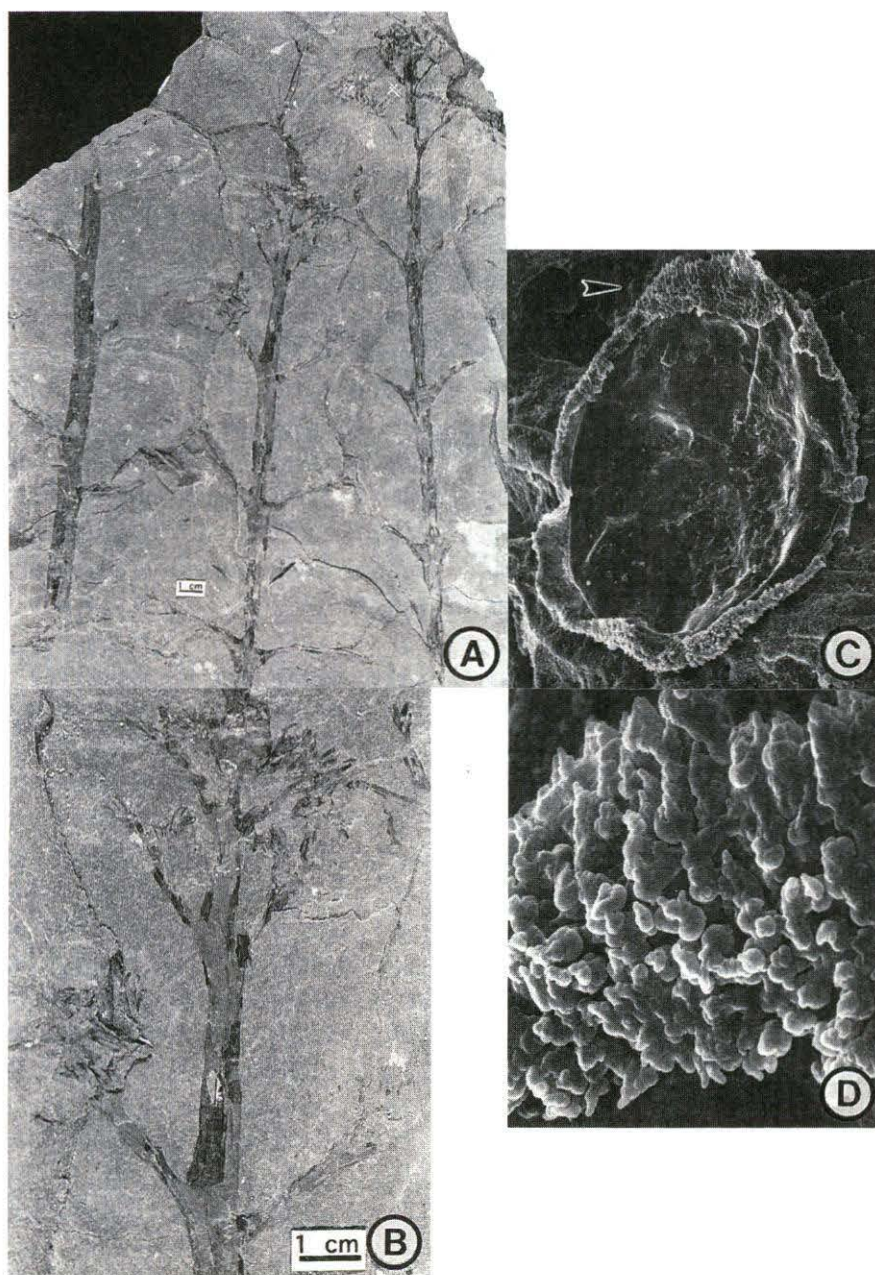


Figure 11.17.

A: Large trimerophyte from probable type locality of "*Psilophyton*" *robustius* Dawson 1871 (further details in appendix). Cap-aux-Os Member, Association 2, Fort Péninsule, GSC 5586. Slab with compressions of three axes, fragment of a once 1.5-m-long slab bearing complete axes, bases curved as though attached to a rhizome (scale, 1 cm). Note alternate lateral branches on specimen to left, opposite-decussate branching on specimen center and right, and sporangia terminating apex as well as lateral branches. $\times 0.3$. **B:** Terminal portion of central axis in (A) (scale, 1 cm). Sporangia borne on lateral and terminal branches appear to be at the same stage of development. Object at top of photograph is an unrelated axis fragment. $\times 0.8$. **C:** Proximal view of spore extracted from sporangium of axis from *Trimerophyton robustius* type locality (SEM). Note partially detached exoexine (which extends across entire distal portion of grain), exposing smooth endoexine and poorly defined trilete aperture beneath. $\times 650$. **D:** Detail of ornamentation of spore in (C) (arrow). Note exoexine comprising more or less conate biform elements seated on very irregular reticulum. $\times 5,000$.

and alternate branching side by side on the same slab (figure 11.17A). The site from which these specimens were collected is apparently the same site from which axes of "*Psilophyton*" *robustius* were collected (Dawson 1871: figure 138; also illustrated in Kräusel and Weyland 1961: pl. 4, figure 1). Opposite-decussate, alternate, and "trichotomous" branching may also be observed on different specimens of the same slab of *Pertica quadrifaria* (paratype, USNM 169002A) and in different specimens of *Pertica dalhousii* (GSC 54741, 54742). In the course of this study, we have maintained the generic distinction, applying the name *Trimerophyton* to those large trimerophytes with smooth axes and relatively lax fertile branchlets (figure 11.17A,B). This appears to be true of the specimens described by Hopping (1956), as well as

the specimen in figure 138 of Dawson (1871), the upper portion of which is in the possession of the Redpath Museum (RM 12.529). We have applied the name *Pertica* to those specimens with sparse to densely scattered, small, acicular trichomes and tightly clustered fertile branches (where present). Slight differences in spore ornamentation visible at the SEM level (figure 11.17C,D) may also distinguish *Trimerophyton* from *Pertica*; however, many more specimens must be examined to determine whether these differences are consistent within genera. Nonetheless, specimens are difficult to assign to one genus or the other, and we believe that these genera require thorough revision to determine whether, in fact, they are distinct, and what characters may be useful to consistently distinguish species.